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Early life history of black sea bass, *Centropristis striata*, in the mid-Atlantic Bight and a New Jersey estuary*

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Abstract.—This study focuses on composite field collections and in situ observations from the mid-Atlantic Bight continental shelf and a New Jersey estuary in order to elucidate aspects of the early life history of age 0+ black sea bass, *Centropristis striata*. Spawning in the mid-Atlantic Bight is prolonged (April through November, with a peak between June and September) and is most intense in the southern portion of this range. Between 1977 and 1987, larvae were collected between Cape Hatteras, North Carolina, and Long Island, New York. In New Jersey coastal waters larvae first appear in July but can occur into November. Recently settled individuals (15–24 mm total length [TL]) were collected at an inner continental shelf site and an adjacent estuary from July through October. By fall, fishes from these areas were 18–91 mm TL, and many had moved offshore from New Jersey estuarine waters and other estuaries to inner continental shelf waters between southern Massachusetts and Cape Hatteras. Subsequently, they continued to move offshore and during their first winter, they were concentrated near the shelf or slope break in the southern portion of the mid-Atlantic Bight. Some age 0+ individuals moved back into New Jersey estuaries in early spring, at sizes approximating those of the previous fall (50–96 mm TL). Thus, black sea bass reach relatively small sizes after 12 months of growth partly because little or no growth occurs during their first winter. This year class reached sizes of 78–175 mm TL by midsummer and 134–225 mm TL by the following fall.

During summer, benthic juveniles were collected or observed primarily in a variety of structured habitats. On the inner continental shelf they were found among accumulations of surfclam *Spisula solidissima* valves or among smaller pieces of shell, and occasionally in burrows in exposed clay. While in the estuary, they were collected from areas with a variety of structured habitats, such as shell accumulations in marsh creeks and peat banks. The data suggest that during their first summer, black sea bass have similar densities and growth rates in estuarine and inner continental shelf habitats, and thus both areas serve as nurseries.

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The black sea bass, *Centropristis striata*, is an important component of recreational and commercial fisheries along much of the east coast of the United States (U.S. Dep. Commerce, 1993). Despite its importance we know relatively little of the early life history of this species (Kendall, 1972). The best efforts to date are studies on larval distribution (Cowen et al., 1993), with comments on presumed estuarine nursery areas (Kendall, 1972), and studies on seasonal distribution and size attained at different seasons (Musick and Mercer, 1977) as well as at the end of the first year (Briggs, 1978). Faunal surveys in the mid-Atlantic Bight from Massachusetts (Lux and Nichy, 1971), New York (Perlmutter, 1939), New Jersey (Bean, 1888; Nichols and Breder, 1927), Maryland (Schwartz, 1961, 1964a), and Virginia (Hildebrand and Schroeder, 1928) have also contributed to our understanding of the seasonal distribution of juveniles. A general summary of the biology, population size, and fisheries is provided by Kendall and Mercer (1982).

In this study we limit our observations to black sea bass in the mid-Atlantic Bight, the area between Cape Cod and Cape Hatteras, because this population is considered a separate stock from those south of Cape Hatteras, North Carolina (Mercer, 1978; but see Bowen and Avise, 1990). This interpretation appears to be supported by studies that show movements inshore and north in spring and offshore and south in the fall within the mid-Atlantic Bight (Pearson, 1932; Nesbitt and Neville, 1935; Lavenda, 1949; June and Reintjes, 1957; Frame and Pearce, 1973) but only localized movements in the South Atlantic Bight (Parker, 1990; Low and Waltz, 1991). Recently, variations in meristic and morphometric characteristics have led to the suggestion that stock structure may not be homogenous within the mid-Atlantic Bight (Shepherd, 1991).

The objectives of this study are to elucidate aspects of the reproduc-

* Contribution 94-30 of the Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ.

tive periodicity, seasonal distribution, growth, and nursery habitats during the first year (age 0+) of black sea bass. We used composite data from a variety of field collections for larvae and juveniles, in situ observations on the mid-Atlantic Bight continental shelf, and intensive collections from a New Jersey estuary.

Materials and methods

Data sources for planktonic larvae and benthic juveniles (age 0+) from the mid-Atlantic Bight (Fig. 1) and southern New Jersey (Fig. 2) are summarized in Table 1. Larval sampling was conducted as part of the National Marine Fisheries Service (NMFS) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) surveys (Sherman, 1980, 1986). Further details of the sampling methodology are provided by Sibunka and Silverman (1984, 1989) and Morse et al. (1987). Larval distribution and abundance are displayed as average number of larvae per 10 m^2 of sea surface calculated by month for the mid-Atlantic Bight study area for 1977–87. Larvae were also collected as part of a characterization of the Long-term Ecosystem Observatory (LEO-15) around Beach Haven Ridge off southern New Jersey (von Alt and Grassle, 1992) (Fig. 2). Samples were collected with an opening and closing Tucker trawl (1-m^2, 505-μ mesh) with multiple codends that were fished in a step-oblique manner from the surface to near bottom for 7.5–15 minutes. The mouth of the net was equipped with a flowmeter to determine the volume of water sampled.

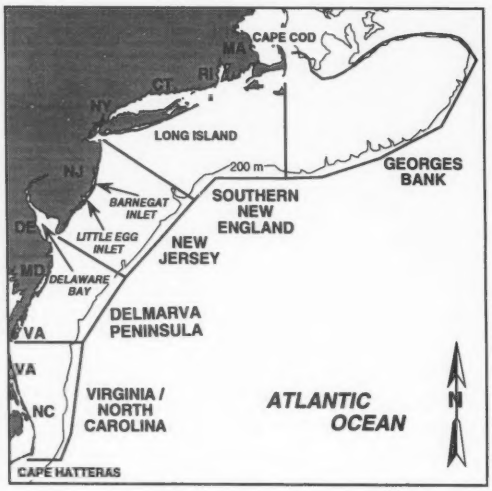

Figure 1

Collection sites for larval and juvenile black sea bass, *Centropristis striata*, in the mid-Atlantic Bight.

Age 0+ juveniles, as determined from length frequencies, were collected from the mid-Atlantic Bight continental shelf during the NMFS-Northeast Fisheries Science Center (NEFSC) bottom trawl surveys. Samples were collected at stratified random stations between Cape Hatteras, North Carolina, and Nova Scotia on the continental shelf. Details of the sample distribution and technique are provided by Azarovitz (1981). Seasonal sampling occurred during fall (September–October), winter (January–February) and spring (March–April). After additional depths were stratified, random sampling occurred seasonally with otter trawls in inshore continental shelf waters off Massachusetts by the Massachusetts Division of Marine Fisheries (MADMF) (Howe, 1989) and off New Jersey by the New Jersey Department of Environmental Protection (NJDEP) (Byrne[1]; Byrne et

[1] Byrne, D. M. 1988. Inventory of New Jersey's coastal waters. New Jersey Division of Fish, Game, and Wildl., Trenton, NJ, 3 p.

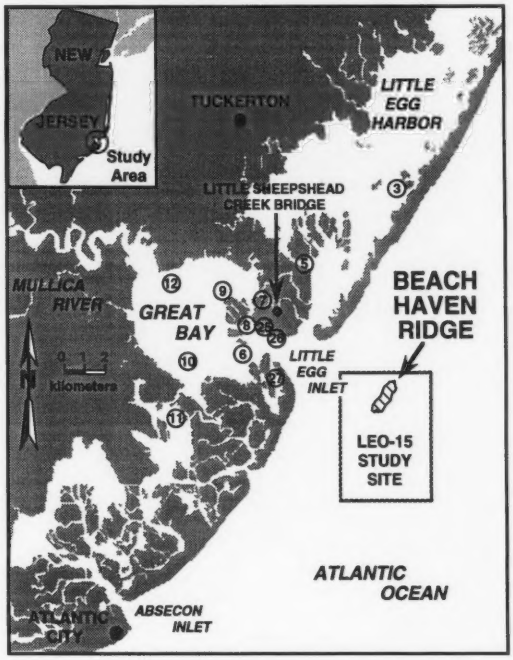

Figure 2

Collection sites for larval and juvenile black sea bass, *Centropristis striata*, from inner continental shelf and estuarine study areas off southern New Jersey. Circled numbers indicate otter trawl sampling sites; number 25, however, is the location of trapping sites at Rutgers University Marine Field Station. Little Sheepshead Creek is the location of the plankton sampling site. LEO-15 = Long-term Ecosystem Observatory.

Table 1

Summary of data sources for larval and juvenile (age 0+) black sea bass, *Centropristis striata*, examined during this study. See Figures 1 and 2 for study areas.

Study area	Sampling method	Sampling period	Sampling depths	Frequency of sampling	Sources
Great Bay–Little Egg Harbor, New Jersey	Plankton net (1 m, 3-mm mesh)	1989–91	0–4 m,	Weekly	Witting, Able, and Fahay, unpubl. data
	Otter trawl (4.9 m, 6-mm mesh codend)	1989–91	1–8 m	Monthly	Szedlmayer and Able[1]
	Traps (6-mm mesh)	1991–92	1-3 m	Daily-weekly	This study
Vicinity of Beach Haven Ridge, off southern New Jersey	Tucker trawl (1 m, 1-mm mesh)	1991–92	0–15.5 m	Bimonthly-monthly	This study
	Beam trawl (2 m, 6-mm mesh)	1991–92	6–23.5 m	Bimonthly-monthly	This study
	Otter trawls (7.6 m, 13-mm mesh codend)	1974	2–19 m	Monthly	Milstein and Thomas, 1977
	In situ observations with SCUBA	1992	10–20 m	Variable during summer	This study
Mid-Atlantic Bight	Otter trawl (10.4 m, 12.5-mm mesh)	1982–90	9–365 m	Seasonal	Azarovitz, 1981
	Bongo plankton nets (61 cm, 505-μ mesh)	1977–87	8–1,500 m	Monthly-bimonthly	Sibunka and Silverman, 1984
Nearshore off Massachusetts	Otter trawl (15 m, 12-mm mesh codend)	1982–90	7–147 m	Seasonal	Howe, 1989
Nearshore off New Jersey	Otter trawl (30 m, 6-mm mesh codend)	1988–91	5–27 m	Seasonal	Byrne (Footnotes 1 and 2 in the text)

[1] Szedlmayer, S. T., and K. W. Able. Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. In review.

al.[2]). More temporally intensive sampling with beam trawls (2-m, 6-mm mesh) was conducted outside Little Egg Inlet in southern New Jersey in the vicinity of Beach Haven Ridge at the LEO-15 site (Fig. 2). Additional length-frequency information was adapted from an environmental impact study in 1974 at this site (Table 1). In the Great Bay-Little Egg Harbor estuarine system (Fig. 2), juveniles were collected with otter and beam trawls and traps over several years in a variety of habitats and depths (Table 1). For all samples, larval size was recorded as notochord length (NL) or standard length (SL), and juveniles as total length (TL).

Visual observations and video records of juveniles and available habitat at several locations in the study area in inner continental shelf waters were made during 1991 and 1992 (Table 1). Near Beach Haven Ridge, 30-m transects were made across a variety of habitat types during 1992.

[2] Byrne, D. M., A. W. Burnett, and D. J. Vareha. 1990. Inventory of New Jersey coastal waters. New Jersey Div. Fish, Game, and Wildl., Trenton, NJ, 39 p.

Results

Temporal and spatial distribution of larvae

Black sea bass reproduction throughout the mid-Atlantic Bight occurs over a fairly prolonged period on the basis of occurrence of larvae from April through November (Fig. 3; Table 2). It appears that reproduction progresses seasonally from south to north on the basis of collections off Virginia and North Carolina as early as April, and off New Jersey and Long Island beginning in July (Fig. 3). The smallest larvae (2–3 mm NL) occurred off New Jersey from July through October (Table 3). At Beach Haven Ridge off southern New Jersey, larvae (4–12 mm TL) were collected in late July and early August.

Larvae occurred in samples from April through November and into January in the mid-Atlantic Bight, although their occurrence varied with geographic location (Table 2; Fig. 3). For all regions, the peak in abundance was from July through September or October (Table 2). The largest larvae collected

Table 2

Abundance of black sea bass, *Centropristis striata*, larvae in the mid-Atlantic Bight expressed as no./10 m^2 of sea surface by month and area during 1977–87. Areas are indicated in Figure 1.

Area	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Georges Bank									6		
Southern New England				4	22	88	42				
New Jersey			7		110	370	150	216	5		
Delmarva				79	376	1672	670	15	8		
Virginia/North Carolina		126	76	100	534	1561	502	53	16		20

Table 3

Monthly totals of black sea bass, *Centropristis striata*, larvae by length collected over the continental shelf off New Jersey during 1977–87. Total number of stations refers to collections containing black sea bass larvae.

		Length (mm NL)									
Month	Total number of stations	2	3	4	5	6	7	8	9	10	Total number of larvae
April	—										
May	1								1		1
June	—										
July	12		3	5	7	3		1			19
August	31	15	66	36	18	13	3	1			152
September	18	2	22	13	6	5	3			1	52
October	13	3	23	12	11	10	2				61
November	2						1	1			2
Totals	77	20	114	66	42	31	9	3	1	1	287

were 8–10 mm NL but most were <8 mm NL. The larvae were distributed across much of the mid-Atlantic Bight continental shelf; the greatest abundance occurred between Cape Hatteras and Delaware Bay (Fig. 3). At the northern limit of occurrence, off New Jersey and Long Island, larvae were most abundant on the inner half of the continental shelf. Only a few larvae were found north and east of the eastern end of Long Island (July, Fig. 3). A single 6.4-mm larva was collected on Georges Bank in November 1982. During weekly night-time sampling in the Great Bay estuary at a site just inside Little Egg Inlet, New Jersey (Table 1; Fig. 2), larvae were never collected during the period from 1989 to 1991 (Witting et al.[3]).

[3] Witting, D. A., K. W. Able, and M. P. Fahay. Marine Field Station, Institute of Marine and Coastal Science, Rutgers Univ., Tuckerton, NJ 08087. Unpubl. data.

Temporal and spatial distribution of benthic juveniles

Benthic age 0+ individuals smaller than 25 mm TL were collected from both inner continental shelf (Beach Haven Ridge) and estuarine (Great Bay) habitats from July through October (Figs. 4–6). Collections from these areas indicate that two length modes occurred during the summer and fall of 1992. The first mode appeared in late July and could be followed through the fall when the fish have reached lengths >50 mm TL. The second mode appeared at the inner shelf site in late September at sizes >10 mm TL. This group reached an apparent minimum size of 30 mm TL by the fall (Fig. 4).

Movement out of the estuary in the fall is indicated by the reduction in the number of age 0+ individuals by November-December (Figs. 4–6). This same pattern of movement out of the estuary also was reflected in the catch per unit of effort (CPUE)

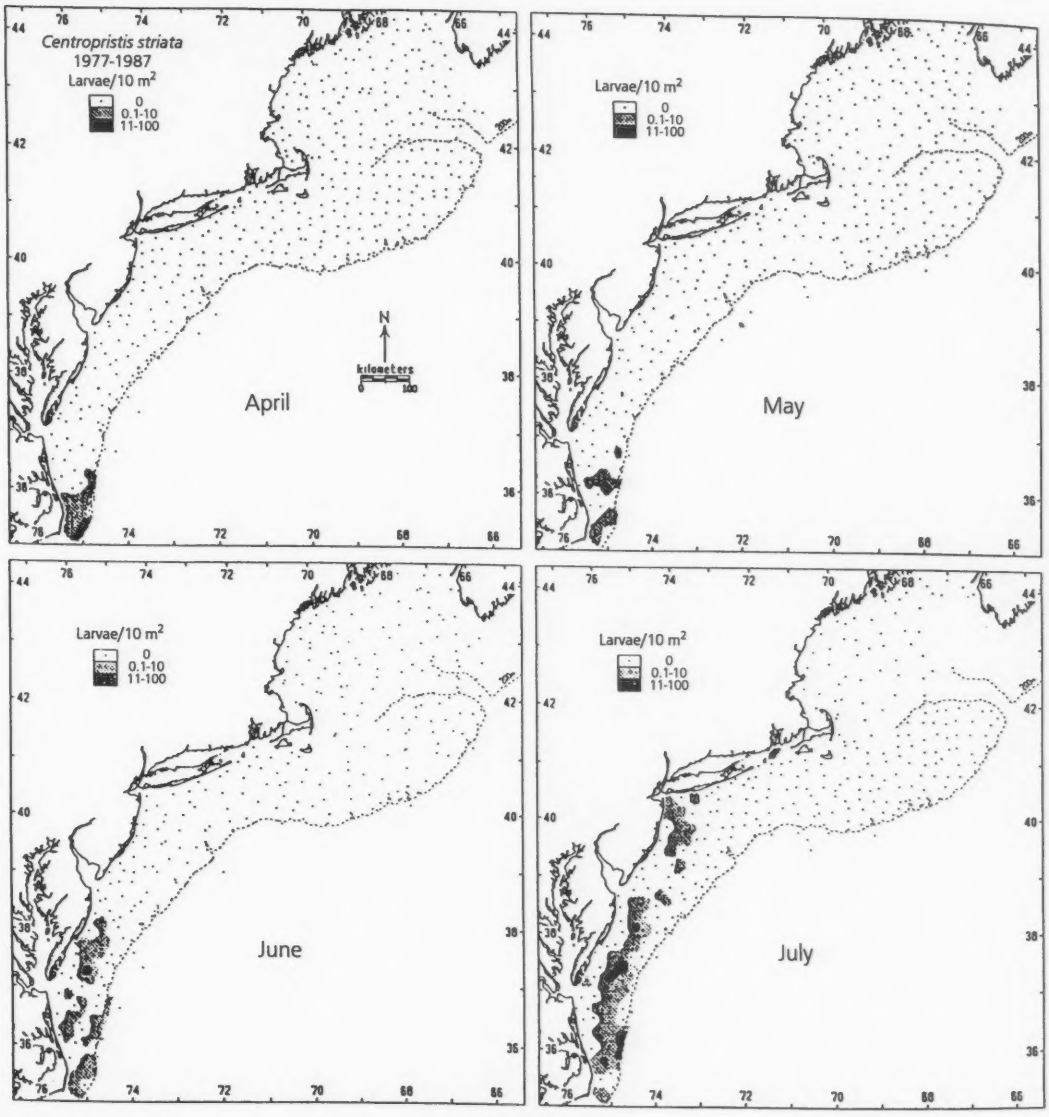

Figure 3

Monthly distribution and abundance of black sea bass, *Centropristis striata*, larvae in the mid-Atlantic Bight based on NMFS-MARMAP surveys during 1977–87.

from trap collections in the Rutgers University Marine Field Station (RUMFS) boat basin in 1992 (Fig. 7). At the same time, catch rates increased dramatically, compared with those for summer, on the inner continental shelf off New Jersey (Fig. 8), owing, presumably, to the addition of individuals moving from the estuary as well as to recently settled fishes. Age 0+ individuals were absent in the winter. Catches at Beach Haven Ridge were zero from December through February and few individuals were caught in March (Fig. 7) in 1991 and 1992. Catches increased in April or May, or during both months, depending on the year, and then decreased through the spring and early summer. This same general seasonal pat-

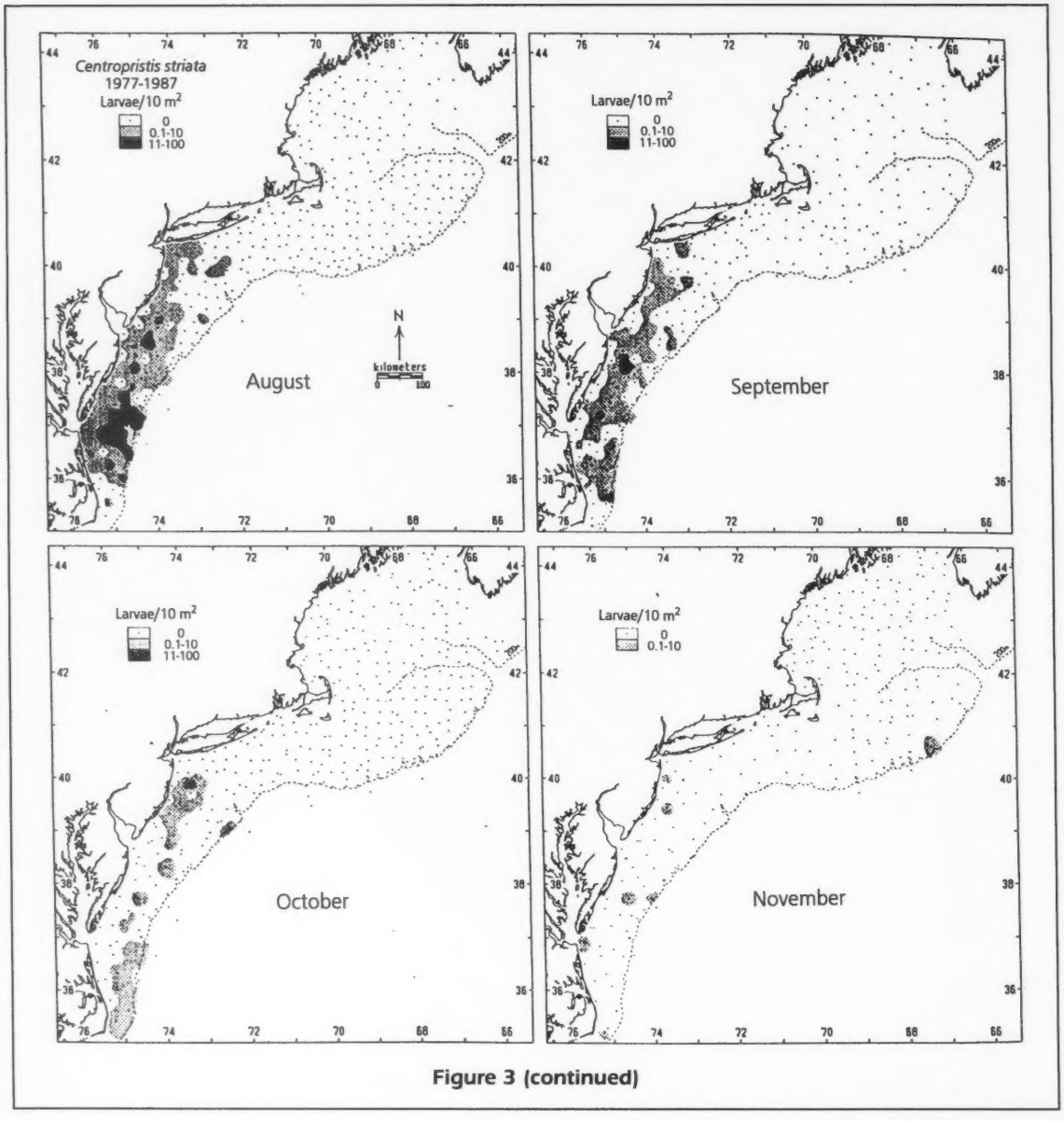

Figure 3 (continued)

tern occurred in the Great Bay estuary between 1988 and 1992 (Fig. 5) and during 1974 (Fig. 6) when most individuals were present from March through May and from August through November and were absent during the winter.

Fall otter trawl sampling from the continental shelf off New Jersey (Fig. 8) and from elsewhere in the mid-Atlantic Bight (Fig. 9) collected age 0+ individuals of the same lengths (3–9 cm TL) as those in the fall estuarine sampling (September and October, Figs. 4–6). These individuals were distributed throughout the inshore portions of the mid-Atlantic Bight (Figs. 8 and 10). Interestingly, the largest collections of age 0+ individuals were taken off eastern Long Island, Rhode Island, and off Massachusetts, both north and south of Cape Cod (Fig. 10). These are areas where larvae were virtually absent in extensive collections between 1977 and 1987 (Fig. 3).

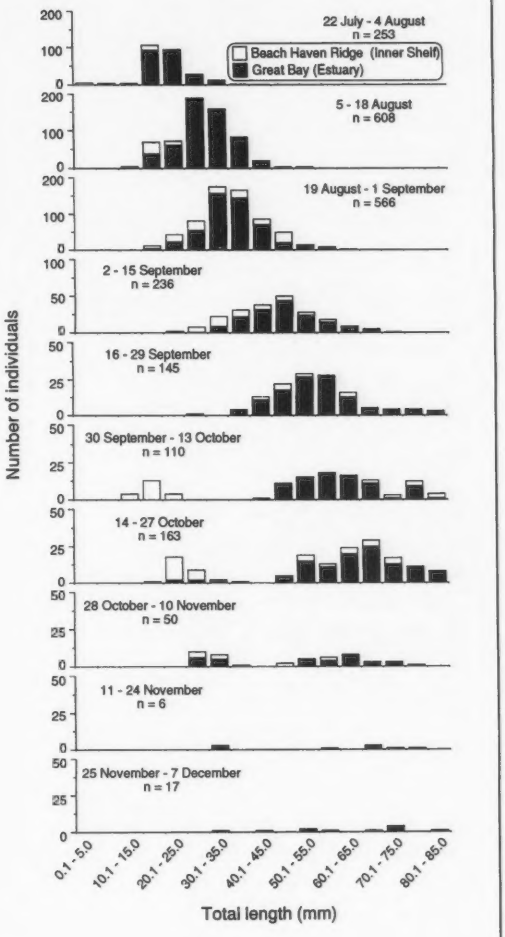

Figure 4

Occurrence and length of black sea bass, *Centropristis striata*, larvae and juveniles collected near Beach Haven Ridge (in plankton, beam trawl, and trap samples) on the inner continental shelf and in the Great Bay estuary (in trap samples) during 1992. See Figure 2 for localities.

Large numbers of 0+ individuals were found in intensive fall surveys in shallower inner continental shelf waters off Massachusetts (Figs. 9 and 10). In the winter, no age 0+ individuals were collected in inner continental shelf waters off New Jersey (Figs. 8 and 10). Most individuals in the winter (January–February) offshore surveys were collected near the edge of the continental shelf. In spring (March–April) surveys over the continental shelf, age 0+ individuals were evident over most depths. Most of these fish were found south of Delaware Bay (Fig. 10), some at a variety of depths off New Jersey. No individuals were collected in inshore spring (April–May) surveys of Massachusetts coastal waters.

Growth

The 1992 year class attained sizes of 18–101 mm TL by October after spawning, which occurred primarily in August (Figs. 4 and 5; Tables 2 and 3). Our estimates of growth rate are confounded somewhat by the occurrence of two length modes of 0+ benthic juveniles (Fig. 4), but calculations, based on the progression of these modes through October, yielded growth rate estimates of 0.45 mm/day for the first and 0.42 mm/day for the second length mode. The 1974 year class appeared to have reached similar lengths by the fall (Fig. 6). In both 1974 and in more recent year classes, sizes of fall fish and those reappearing the following spring were similar (Figs. 5 and 6), indicating very little growth over the intervening winter.

Growth resumed at a relatively fast rate in the spring and continued through the summer. Based on monthly increases (April–September, Fig. 5) in mean size, growth rate was 0.77 mm/day during the period. By July, approximately one year after spawning, these fish were 70–180 mm TL (Fig. 5). By September, when these fish were approximately 14–17 months old, they were 134–251 mm TL. A similar pattern was evident for 1974 (Fig. 6).

Habitat

Juveniles (age 0+) were collected and observed in a variety of habitat types both on the continental shelf and in the estuary. Densities of age 0+ individuals were similar between the inner continental shelf (Beach Haven Ridge) and estuarine study sites in the fall (August and September). When all the values for all habitats were combined, they were virtually identical with 0.33 (±0.007) ind·m^{-2} in the estuary (1-m beam trawl, n=144) and 0.32 ind·m^{-2} (±0.006) on the inner continental shelf (2-m beam trawl, n=57) (Table 1). Age 0+ individuals, both on the inner shelf and in the estuary, were found in habitats with some structure. Visual observations and video records provided evidence that individuals occurred in large linear accumulations or "windrows" of the Atlantic surfclam valves, *Spisula solidissima,* during the day in depths of 14–20 m on the inner continental shelf near Beach Haven Ridge in 1991 and 1992 (Petrecca[4]). Estimates made from video-

[4] Petrecca, R. Institute of Marine and Coastal Sciences, Rutgers Univ., New Brunswick, NJ 08903. Personal commun., 1992.

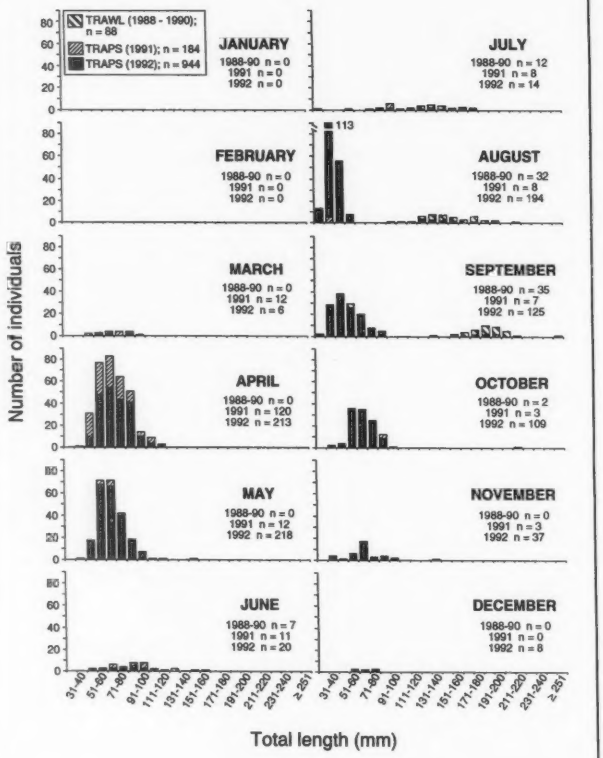

Figure 5

Monthly length frequencies of black sea bass, *Centropristis striata*, from the Great Bay-Little Egg Harbor estuarine system during 1988–92.

tapes taken during 1991 indicated that there were as many as five individuals/m^2 in the surfclam shell habitat. During the same periods they were not observed in adjacent open sand bottom, sand with pronounced megaripples, nor in exposed clay substrate habitats. In situ observations at other locations found age 0+ individuals at a number of continental shelf sites off Barnegat Inlet, New Jersey, in 19–26 m depths. In many of these instances the juveniles were associated with broken mollusk shells on the bottom and were seldom seen over sand substrate without shells (Witting[5]).

In the Great Bay-Little Egg Harbor estuary system (Fig. 2), patterns of habitat use for age 0+ black sea bass were derived primarily from beam trawl catches in 1992 (Fig. 11). They were most abundant in habitats (Fig. 2) with sand and shell (Stn. 5) and in habitats with sand with seasonally varying amounts of amphipod (*Ampellisca*) tubes (Stn. 9). They also occurred frequently in channels with silt substrate (Stn. 10), over silt and shell (Stn. 12), over bare sand (Stn. 8), over sand with seasonally occurring macroalgae (*Ulva lactuca*) (Stn. 11), in marsh creeks (Stns. 25–27), and were less abundant in an area with extensive hydroids (Stn. 6). They were absent in eelgrass (*Zostera marina*, Stn. 3) and in a habitat mixture of sand, shell, sponge, and peat (Stn. 7). All of these habitats were located at depths of 1–8 m in the polyhaline portion of the lower estuary. Separate trap sampling in marsh creeks directed at deep holes (2–3 m) confirmed the presence of age 0+ individuals in these holes but not in uniform, shallow areas (approx. 1 m).

Temperatures of areas where juvenile black sea bass occurred varied seasonally. In the estuary at

[5] Witting, D. A. Marine Field Station, Institute of Marine and Coastal Sciences, Rutgers Univ., Tuckerton, NJ 08087. Personal commun., 1994.

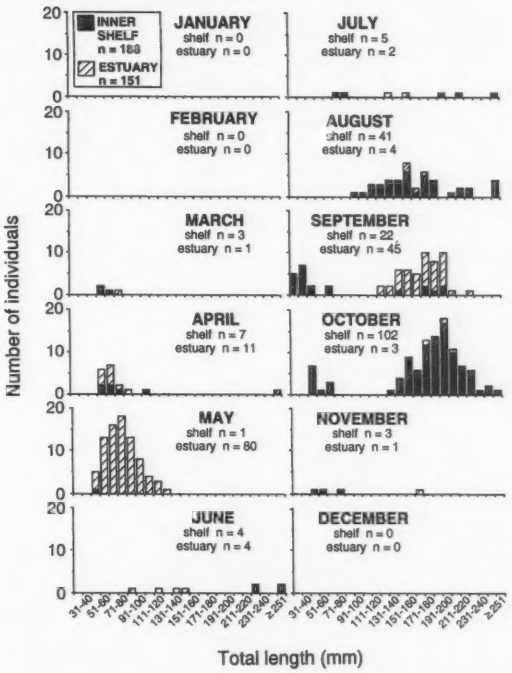

Figure 6

Monthly length frequencies, based on otter trawl collections, of black sea bass, *Centropristis striata*, from the inner continental shelf in the vicinity of Beach Haven Ridge and Great Bay-Little Egg Harbor estuary during 1974.

the time of first spring collections, temperature was approximately 10°C for individuals age 1+ (approximately 9 months old), whereas in the summer temperature was approximately 23°C for age 0+ individuals (Fig. 7). In the vicinity of Beach Haven Ridge, the age 0+ individuals first occurred at approximately 15°C and were most abundant when bottom temperatures reached 20°C (Fig. 7). Over the continental shelf in the fall, the age 0+ cohort was collected primarily at bottom temperatures of 14–17°C (Fig. 12) and at higher average temperatures of 16–21°C in Massachusetts inshore waters (Fig. 12). During winter, most individuals were collected at 6–9°C (Fig. 12), a temperature that probably reflects their greater abundance in deeper waters at that time (Fig. 10). In the spring, this same cohort was abundant at 6–11°C and 15–17°C. In every instance on the continental shelf, with the possible exception of inshore Massachusetts, the fish were found at higher average temperatures than those represented by most of the stations sampled (Fig. 12).

Discussion

Annual cycle in the early life history

Spawning of black sea bass in the mid-Atlantic Bight proceeds from south to north, presumably with warming temperatures. Our interpretation of this geographical pattern is based on extensive collections during 1977–87 and is consistent with that reported for 1966–67 (Kendall, 1972; Kendall and Mercer, 1982). The occurrence of larvae of all sizes in all areas suggests that spawning and development occurs throughout most of the mid-Atlantic Bight. In addition, most larvae were <8 mm TL in our continental shelf collections and were similar to those

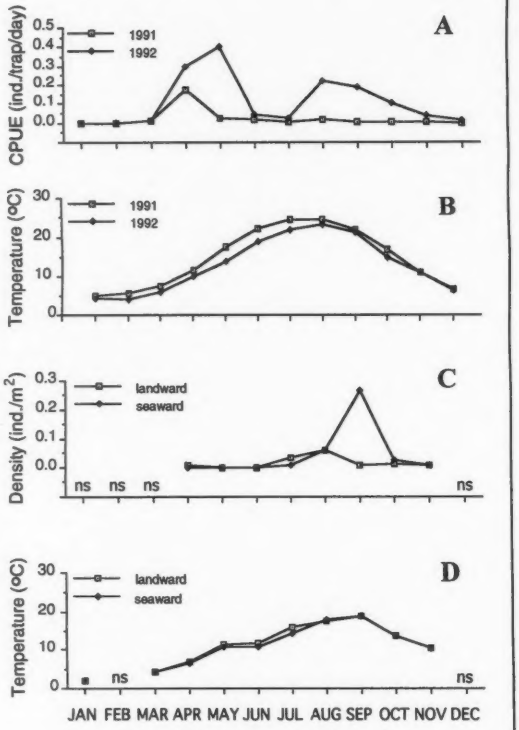

Figure 7

Monthly averages of abundance of age 0+ black sea bass, *Centropristis striata*, and temperature in the estuary (**A** and **B**) and on the inner continental shelf in the vicinity of Beach Haven Ridge (**C** and **D**). Abundance was based on trap collections in the estuary and on beam trawl sampling landward and seaward of the ridge.

reported by Kendall (1972). Thus, black sea bass may settle to the bottom at sizes between 10 and 16 mm TL. This size range also corresponds to the size at which ossification of fin rays and vertebrae is completed (Kendall, 1972). The smallest individual previously reported from the continental shelf was one of 43 mm (Massman et al., 1962). Settlement on the inner continental shelf and in the estuary occurred from July through October according to our estimations based on collections of small individuals (<20 mm TL) throughout that period (Fig. 4). The identification of two length modes during 1992 in both the estuary and on the inner continental shelf (Fig. 4) was not as obvious at the same continental shelf location in 1991 when small juveniles (10–20 mm TL, n=35) occurred from August through October. On the basis of consistent occurrence of age 0+ individuals, it is evident that both the inner continental shelf and estuaries function as nurseries (see below) during the first summer and fall.

Black sea bass (age 0+) appear to leave the estuary and the inner continental shelf off New Jersey during the fall and to move to deeper waters as indicated by the decline in CPUE in the estuary, by the simultaneous increase in numbers on the inner shelf, and by the subsequent complete disappearance of fish from both of these areas by winter. This pattern is evident on the continental shelf throughout the mid-Atlantic Bight from fall collections of the same year class, especially south of Delaware Bay (Fig. 10) as previously observed (Musick and Mercer, 1977). These movements are likely initiated in the fall by decreasing temperatures as suggested by the decrease in fish abundance with declining estuarine

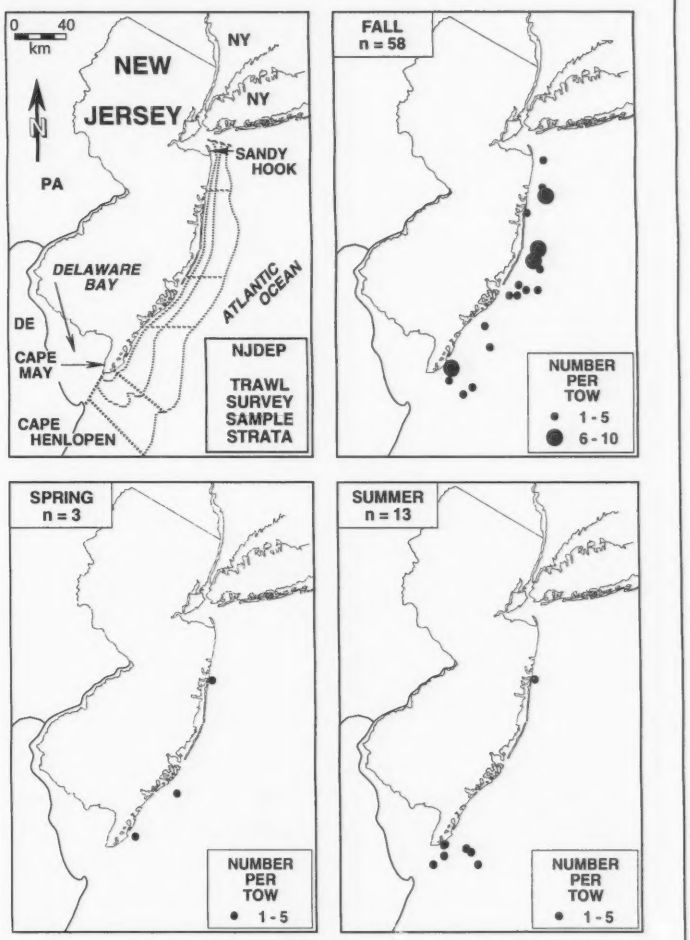

Figure 8

Distribution of age 0+ black sea bass, *Centropristis striata*, during the fall, spring, and summer in inner continental shelf sampling areas off New Jersey during 1988–91. No fish were collected during winter.

temperatures (Fig. 7). This same trend was also noted in Chesapeake Bay estuaries (Musick and Mercer, 1977) and off the coast of Massachusetts (Lux and Nichy, 1971). This response is not surprising given the inability of young (Schwartz, 1964b) and age 0+ (Hales and Able, in press b) black sea bass to tolerate temperatures below 2–3°C, which can occur in the Great Bay estuary during the winter (Able et al., 1992; Szedlmayer et al., 1992). Age 0+ individuals apparently spend the winter on the outer continental shelf, but by early spring they can be found over most of the shelf (Fig. 10). Musick and Mercer (1977) have suggested that they overwinter on the continental shelf in somewhat shallower depths (56–110 m). This year class reenters New Jersey estuaries in the spring, where it spends the summer, then migrates offshore again in the fall. A similar seasonal pattern occurs in Chesapeake Bay estuaries (Musick and Mercer, 1977, and references cited therein).

The 70–180 mm TL size range attained during the first year (ending July) is similar to that reported from back-calculated lengths from scales (approximately 40–159 mm TL; Briggs, 1978) and otoliths (75–107 mm SL; Alexander, 1981). The 1+ age class

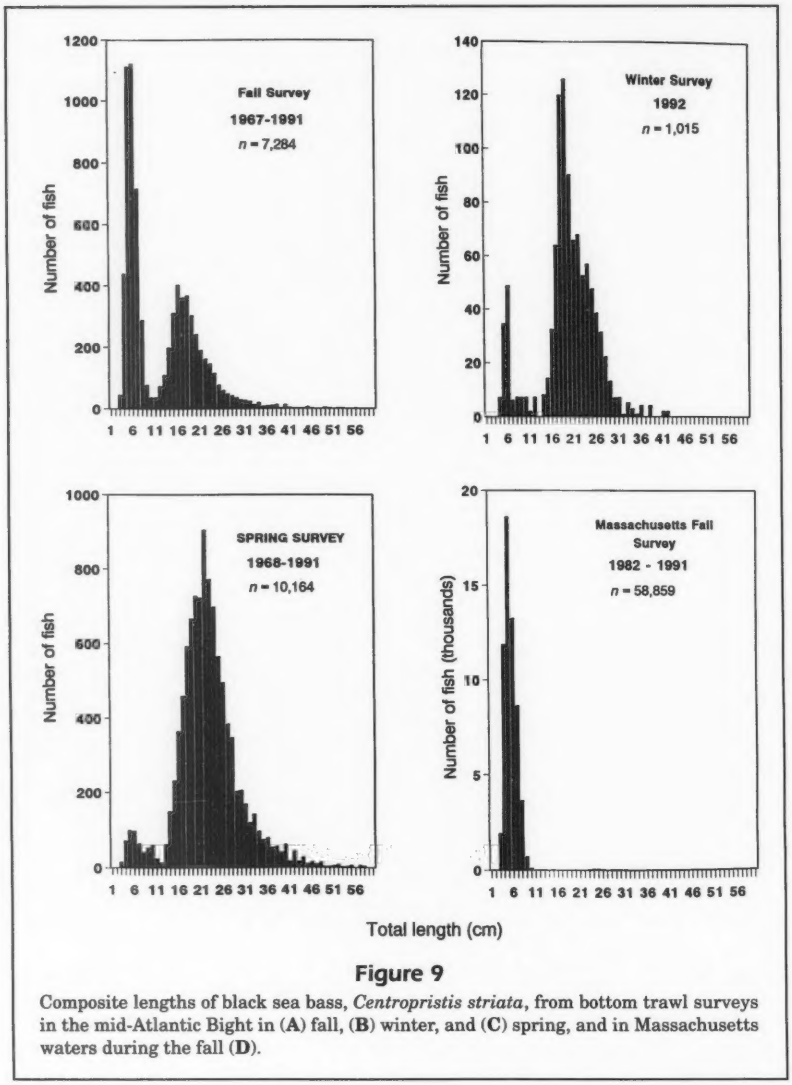

Figure 9

Composite lengths of black sea bass, *Centropristis striata*, from bottom trawl surveys in the mid-Atlantic Bight in (**A**) fall, (**B**) winter, and (**C**) spring, and in Massachusetts waters during the fall (**D**).

appears to follow a similar pattern of inshore-offshore movements as indicated by catches in the estuary over a number of years (Figs. 5 and 6). Thus this annual pattern may be characteristic for age 0+ and 1+ black sea bass for the entire mid-Atlantic Bight.

Nursery habitats

There are inconsistencies between the available data on larval distribution and presumed nursery areas in southern New England. The northern limit of larvae from MARMAP samples for the period 1977–87 was off Long Island (Fig. 3). Earlier studies noted the absence of black sea bass larvae from Block Island Sound (Merriman and Sclar, 1952), Narragansett Bay (Bourne and Govoni, 1988), Long Island Sound (Wheatland, 1956; Richards, 1959), Great South Bay, Long Island (Monteleone, 1992), and offshore of these areas (Kendall, 1972). The only exception was the collection of a few larvae from Georges Bank (Table 2), Cape Cod Bay (Scherer, 1984), and Narragansett Bay (Herman, 1963). However, there was some documentation of spawning aggregations in southern Massachusetts coastal waters (Wilson, 1889).

Despite the scarcity of larvae in southern New England, age 0+ individuals have been very abun-

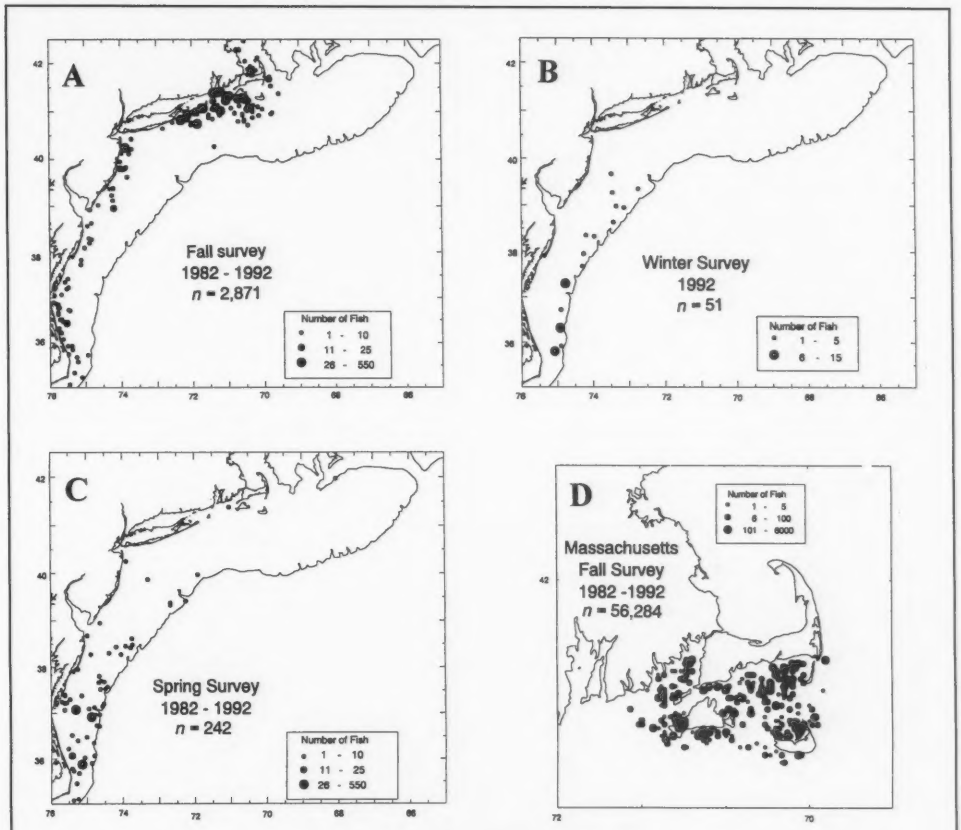

Figure 10

Distribution of age 0+ black sea bass, *Centropristis striata*, in the fall, winter, and spring based on composite collections (1982–92) from the mid-Atlantic Bight and in the fall off the coast of Massachusetts (1982–92).

dant in nearshore waters off Massachusetts (Fig. 10). The age 0+ year class from some estuaries on the south shore of Massachusetts has been described as either rare (Waquoit Bay-Eel Pond estuary [Curley et al., 1967]) or common (Quisset Harbor and Wareham River [Sumner et al., 1913]; Bass River [Curley et al., 1975]; Little Sippewisset Marsh [Werme, 1981]; Great Harbor near Woods Hole [Lux and Nichy, 1971]). In Bass River, where juveniles represented 9.3% (n=69) of the total catch, they were most abundant in deeper (1–3 m) otter trawl catches from August to October (Curley et al., 1975). In Little Sippewisset Marsh they were found in the channels of shallow marsh creeks (Werme, 1981), and juvenile black sea bass were regularly collected in Buzzards Bay and Vineyard Sound during the autumn bottom trawl survey (Fig. 10). The abundance of age 0+ individuals in the region indicates that further

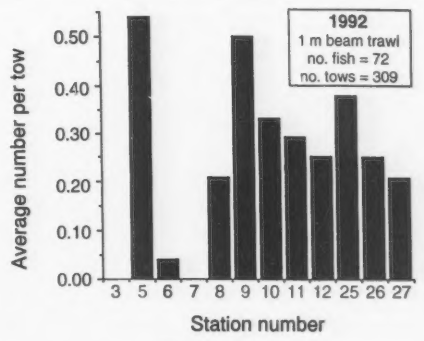

Figure 11

Abundance of age 0+ black sea bass, *Centropristis striata*, in the Great Bay-Little Egg Harbor estuary during 1992. See text for habitat designations and Figure 2 for locations.

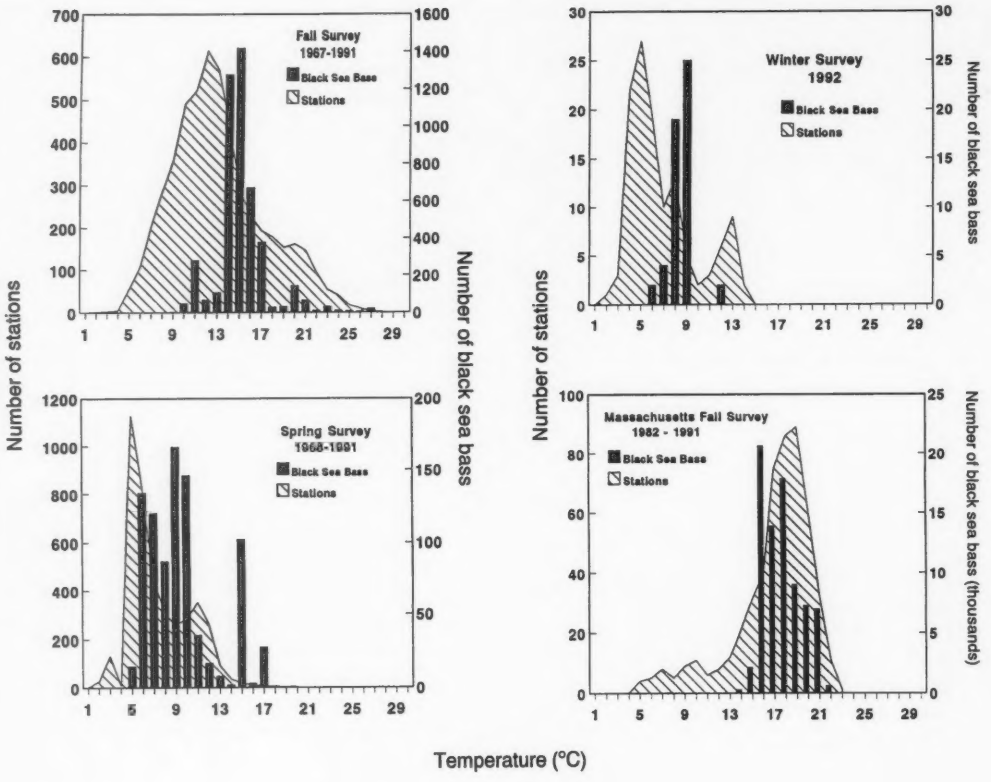

Figure 12

Abundance of age 0+ black sea bass, *Centropristis striata*, relative to bottom temperature in the spring, fall, and winter on the mid-Atlantic Bight continental shelf and off the coast of Massachusetts, based on Northeast Fish. Sci. Cent. and Massachusetts Div. Marine Fisheries bottom trawl surveys (1982–92).

studies are warranted to understand the possible significance of the region as a nursery.

In southern New Jersey, spawning and nursery areas are somewhat better delineated. The larvae clearly occur on the inner continental shelf off New Jersey (Figs. 3 and 4; Kendall, 1972), but there is no evidence of larvae in estuaries and bays in New Jersey (Croker, 1965; Himchak, 1982; Witting[3]) or Delaware (Pacheco and Grant, 1965; Wang and Kernehan, 1979). The apparent absence of larvae in estuaries and the occurrence of larvae and small juveniles (<20 mm TL) at Beach Haven Ridge suggest that settlement may initially occur on the inner continental shelf and that some individuals may remain there while some move into estuaries. Larvae 15–17 mm were reported in late July near Hereford Inlet, New Jersey (Allen et al., 1978), but further details are not available. The only other prior reports of small juveniles in New Jersey estuaries are of 25-mm individuals from Great Egg Harbor (Bean, 1888), 20-mm individuals from Raritan Bay (Nichols and Breder, 1927) and 25–35 mm specimens from lower Delaware Bay (Wang and Kernehan, 1979). The occurrence of juveniles in the York River in Chesapeake Bay (Musick and Mercer, 1977) was based on individuals that may have overwintered on the continental shelf and reentered the estuary as occurs in New Jersey. In other Chesapeake Bay habitats black sea bass (some of them 140–165 mm) were more abundant in eelgrass, *Zostera marina*, both day and night, than in adjacent unvegetated areas (Orth and Heck, 1980).

Our observations suggest that suitable summer nursery habitats, either on the continental shelf or in estuaries, are presumably related to the occurrence of some type of bottom structure, such as peat and shell accumulations. This is further substantiated

by the increase in catch rates of black sea bass juveniles when shell was added to estuarine substrate to improve oyster recruitment (Arve, 1960). Dissolved oxygen also may influence patterns of habitat use because juveniles are intolerant of low levels (Hales and Able, in press a). The similarities in the densities and in sizes attained in the fall by juveniles in the estuary and in the adjacent inner continental shelf suggest that habitat quality is similar for both these areas, if one assumes that size differential predation or movements did not occur at either site during the sampling period. In summary, these data indicate that both estuaries and the inner continental shelf are important as nursery areas and that juvenile black sea bass are not strickly estuarine dependent.

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Population estimates of Pacific coast groundfishes from video transects and swept-area trawls

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Abstract.—Demersal fish surveys are used for two purposes: to detect trends in multispecies communities for environmental assessment and to provide fishery independent stock assessments for management. We compared remotely operated vehicle (ROV) and swept-area trawl surveys to evaluate their strengths and weaknesses for these two purposes. ROV abundance estimates tended to be higher and have lower coefficients of variation than did trawl abundance estimates. This trend is greatest for benthic species and particularly so for small, cylindrically shaped fishes. For patchily distributed, off-bottom fishes such as rockfish, *Sebastes* spp., sablefish, *Anoplopoma fimbria*, and Pacific whiting, *Merluccius productus*, the results vary between ROV and trawl estimates. For environmental assessment, the ROV estimates are superior because, for most species, abundances are higher and smaller changes can be detected. For fisheries management of commercially important species, the results are divided. Dover sole, *Microstomus pacificus*, and thornyheads, *Sebastolobus* spp., have higher ROV abundance estimates and lower coefficients of variation than the trawl. Sablefish, which exhibit more off-bottom behavior, have higher trawl estimates at two of three depths. The ROV and trawl provide different types of information not available from other gear. Much of the difference between the two types of surveys stems from the nature of the sampling gear and from the behavior, body shape, and size of the fishes.

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Estimates of population abundance are essential to research for understanding the impact of human activities on marine demersal fish populations. Traditionally, swept-area trawl surveys have been used to obtain abundance estimates aimed at fisheries management. Recently, environmental surveys, used to monitor the impacts of pollution and coastal development, have become more widespread and important. These two types of surveys have different goals. Data from fisheries surveys are used as input for predictive models to forecast the results of alternative fisheries management strategies and are usually directed toward either a single species or a small species group. Environmental surveys are used to detect trends in populations over time, to distinguish those trends from natural variation, and are usually directed at an entire multispecies fish community.

Both types of survey population estimates are subject to the problems of bias and precision. Bias is a particular problem for fisheries surveys. Fishery stock assessment is based on models that integrate fishery catch-at-age data with fishery-independent survey estimates of abundance (Deriso et al., 1985). The catch-at-age data, sampled from the commercial fishery, document the trend of population change resulting from recruitment of young fish into the population and from removal of individuals out of the population due to fishing and natural mortality. The fishery-independent survey data are used as a measure of either relative or absolute abundance (Doubleday and Rivard, 1981). These survey data are used to calibrate or "tune" the trend ob-

tained from the catch-at-age data to determine how close the population is to a threshold value of overfishing (Kimura, 1989). Survey data also yield valuable information on migration routes, or biological parameters such as age-at-maturity, fecundity, and feeding. Biased survey estimates can result in very precise estimates of population abundance which are either lower or higher than the true population abundance.

For environmental surveys, the problem of precision is the major concern. Here, the goal is to detect a trend in population size, often of all the fish in the habitat, and to distinguish that trend from natural variation in fish populations. Abundance estimates from trawl surveys tend to have very large variances; often means and variances are correlated (see Lenarz and Adams, 1980). Resulting confidence intervals around means range from 50 to 100% for flatfish species and are greater than 100% for rockfish, *Sebastes* spp. (Raymore and Weinberg, 1990). As a result, all but the most extreme changes in population size are masked by these large confidence intervals. Methods commonly used to deal with this variability are transformations using the negative binomial (Lenarz and Adams, 1980) or the Delta distribution (Pennington, 1986). Data transformed by using these distributions often result in the variance being independent of the mean; however, the large confidence intervals and low statistical power remain.

In this study we examined video transects conducted from a remotely operated vehicle (ROV) as an alternative method for making population estimates of demersal fishes and compared these estimates to those from a conventional swept-area trawl survey.

Methods

Study site

The study site off central California lies along a cone-shaped ridge which runs southwest from Santa Cruz, California, and separates Monterey Canyon to the south from Ascension Canyon to the north (Fig. 1). Surface topography of the ridge is smooth and relatively unbroken (Greene[1]). The ridge is composed of sandstone, is covered with mud of pelagic origin, and is characterized by occasional areas of exposed bedrock. The stations where ROV and trawl operations were conducted were located along the ridge at depths of 200, 400, and 600 m (see Fig. 1).

[1] Greene, G. U.S. Geological Service, Pacific Marine Geology, 345 Middlefield Rd., Menlo Park, CA 94025. Personal commun., 1992.

ROV operations

ROV operations were conducted by using the Monterey Bay Aquarium Research Institute's ROV *Ventana* aboard the RV *Point Lobos*. The ROV was equipped with a Sony DXC-3000 video camera with a 5.5–44 mm zoom lens, illuminated by four 400-W sodium scandium lights. The zoom lens was used only for identification off the transect. Fiber-optic cable was used for viewing and recording images. The ROV was also equipped with a combined dual signal, a global positioning system and sonar system, which recorded the ROV position every 10 seconds. Depth, altitude off bottom, and various camera settings were also recorded.

At least three replicate transects were made at each depth. Transects at the 200-m, 400-m, and 600-m depths were sampled (for dates, see Table 1). Because a video transect covering the same total area as a trawl was not practical, a transect length of similar distance covered by a trawl was chosen (approximately 1.8 km or 1 nmi). Strip transects were used rather than line transects because the orientation of the lights produced a very sharp boundary between illuminated width of the transect and the darkness (Burnham et al., 1980; Butler et al., 1991). Transects were made at a speed of approximately 1.8 km/hr (1 knot) parallel to the isobath, interrupted occasionally by stops for fish identification or vehicle maintenance. Transects were made with a camera angle of 30° off the parallel horizon to the bottom and with a camera height averaging 0.7 m off the bottom. Fish were identified from videotapes by two independent viewers, and the response of each fish to the ROV was recorded as follows: 1) strongly attracted (rapidly moving into the frame); 2) weakly attracted

Table 1

Dates of remotely operated vehicle (ROV) and trawl sampling cruises at 200-m, 400-m, and 600-m depth strata off central California. The number in parentheses is the number of transects or trawls occurring during that month.

Depth stratum (m)	ROV	Trawl
200	Oct 1991 (3)	Apr 1991 (2)
		Sep 1991 (3)
		Jan 1992 (3)
400	Mar 1991 (1)	Apr 1991 (1)
	Oct 1991 (1)	Sep 1991 (3)
	Oct 1992 (2)	Jan 1992 (4)
600	Jul 1991 (1)	Apr 1991 (2)
	Sep 1991 (2)	Sep 1991 (4)
		Jan 1992 (3)

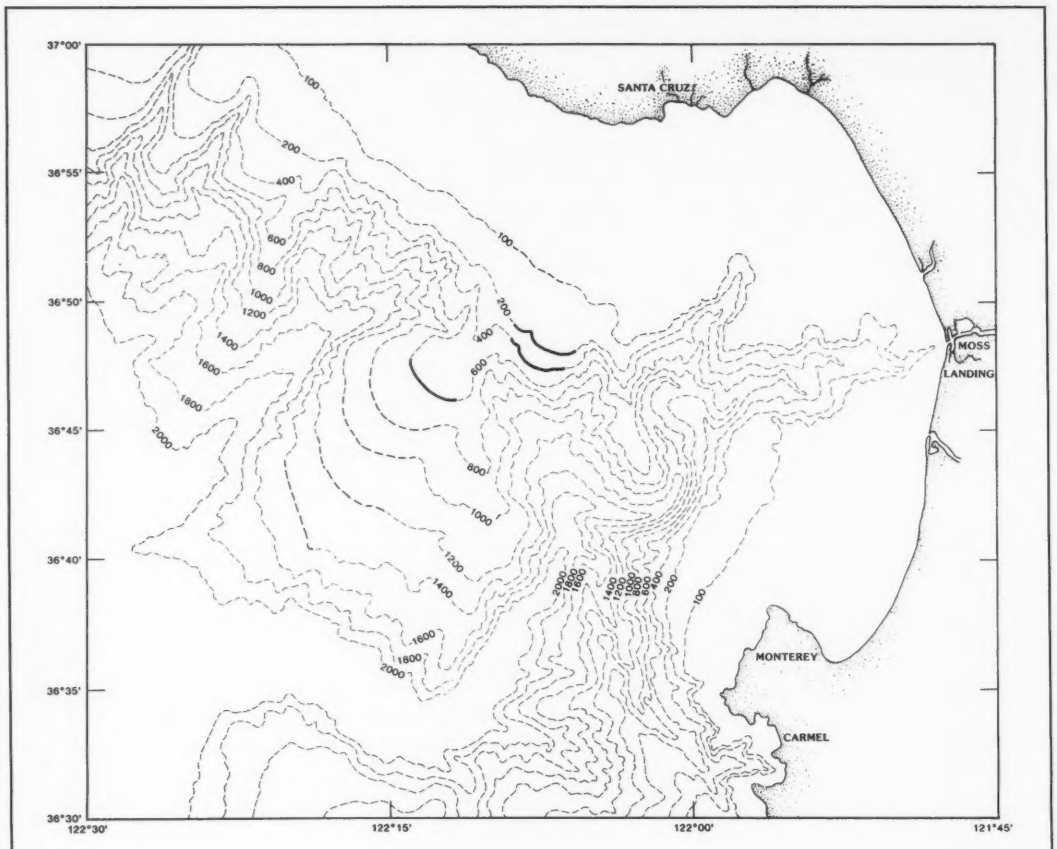

Figure 1

Study site off central California marked for 200-m, 400-m, and 600-m depth comparisons of population estimates from video transects conducted from an ROV survey and from swept-area trawl surveys.

(slowly moving into the frame); 3) no response (no movement); 4) weakly avoided (slowly moving out of the frame); and 5) strongly avoided (rapidly moving out of the frame). A time line, at which the fish were counted, was chosen in the center of the viewing area. To determine transect width at the time line, the ROV was transected over a 5-m square grid, and known lengths from the grid were measured on the monitor. From these lengths and standard photometric equations (Wakefield and Genin, 1987), the transect width was calculated to be 1.8 m (see Fig. 2). The vertical perspective of the video ranged from a height of 0.7 m at the camera to a visual horizon of 2.4 m in front of the ROV. The number of fish per transect was converted to fish per hectare by dividing the number of fish observed by the area covered (transect distance multiplied by transect width).

Trawl operations

Trawling was conducted on separate cruises on the RV *David Starr Jordan*. Three trawl surveys were conducted and a sample size of at least three trawls per station was taken per cruise (for dates, see Table 1). During the April 1991 cruise, all three replicates were not completed owing to inclement weather. Parallel tows were made along the same isobath as the ROV transect at a speed of approximately 3.7 km/hr (2 knots) for 30 minutes, although control of the trawl was not as exact as that of the ROV. The net, an Aberdeen high-rise trawl net with a 29-m (96-ft) headrope, was equipped with 1.5×2.1 m steel doors. Trawl openings were not measured; this type of trawl has an average horizontal opening of 13.5 m (see Fig. 2) and an average vertical opening of 5.5 m

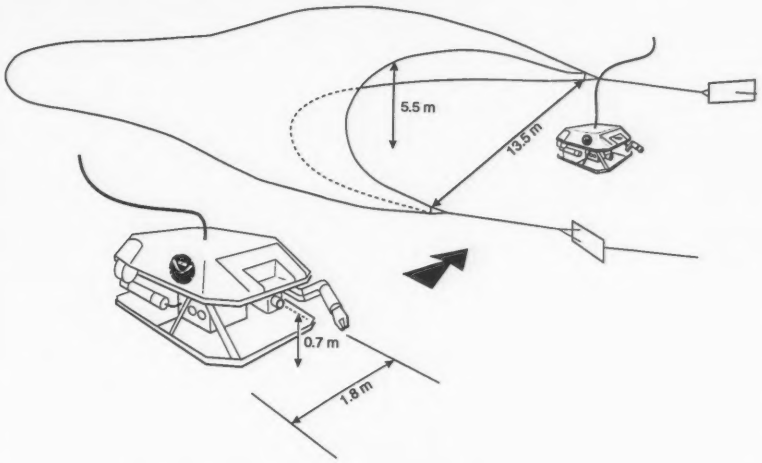

Figure 2

Sampling dimensions of a remotely operated vehicle (ROV) video transect and a trawl. Drawings of gear and sampling volumes are made to scale.

(Rose[2]). On deck, catches were handled with standard protocol (Smith and Bakkala, 1982) and were sorted to species, weighed, and measured. Lengths were measured for either a subsample of 100 fish or the entire catch, if it comprised less than 100 fish. When the catch was greater than 100 fish for a species, total species number was extrapolated from total species weight by using the average weight per fish from the subsample weight and numbers. Numbers of species per hectare were expanded by dividing the total species number by the area covered (distance traveled by a tow multiplied by the average width of the trawl).

Differences in ROV and trawl abundance estimates for individual species at each depth were tested by using t-tests for differences of unpaired log-transformed means. A sign test was used to determine whether the number of times that an ROV abundance estimate (or coefficient of variation) was higher than the trawl was greater than would have been expected randomly (i.e. a 50/50 ratio).

Statistical power is defined as $1-\beta$, where β is the probability of failing to reject a hypothesis when it is false, and therefore power is the probability of correctly rejecting a false hypothesis (Peterman, 1990). The power of the ROV and trawl abundance estimates was evaluated by calculating the required sample size to detect a 50% reduction from the log-transformed mean abundance at a fixed level of α (0.05) and at a high level of power ($1-\beta$, 0.80). Comparisons were made for the commercially important species (Dover sole, *Microstomus pacificus*; thornyheads, *Sebastolobus* spp.; and sablefish, *Anoplopoma fimbria*) and for a group of other abundant taxa (catsharks, Scyliorhinidae; skates, Rajidae; and eelpouts, Zoarcidae) at the 400-m depth (the only depth where all of these taxa occurred in both the ROV and the trawl surveys).

Results

More fish per hectare were observed from the ROV than were captured in the trawl at the 400-m and 600-m depths, whereas more fish were captured in the trawl at the 200-m depth (Fig. 3). However, the differences in the log-transformed total ROV and trawl estimates were only significant at the 400-m and 600-m depths (400 m: t=5.50, P<0.001; 600 m: t=3.28, P=0.011) and not at the 200-m depth (200 m: t=0.32, P=0.713). Numbers captured in the trawl at the 200-m depth were higher owing to a single large catch of two species of rockfish in one trawl. The ROV estimates of fish numbers were higher for most individual species or taxonomic groups that occurred in

[2] Rose, C. National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA, 98115–0700. Personal commun., 1992.

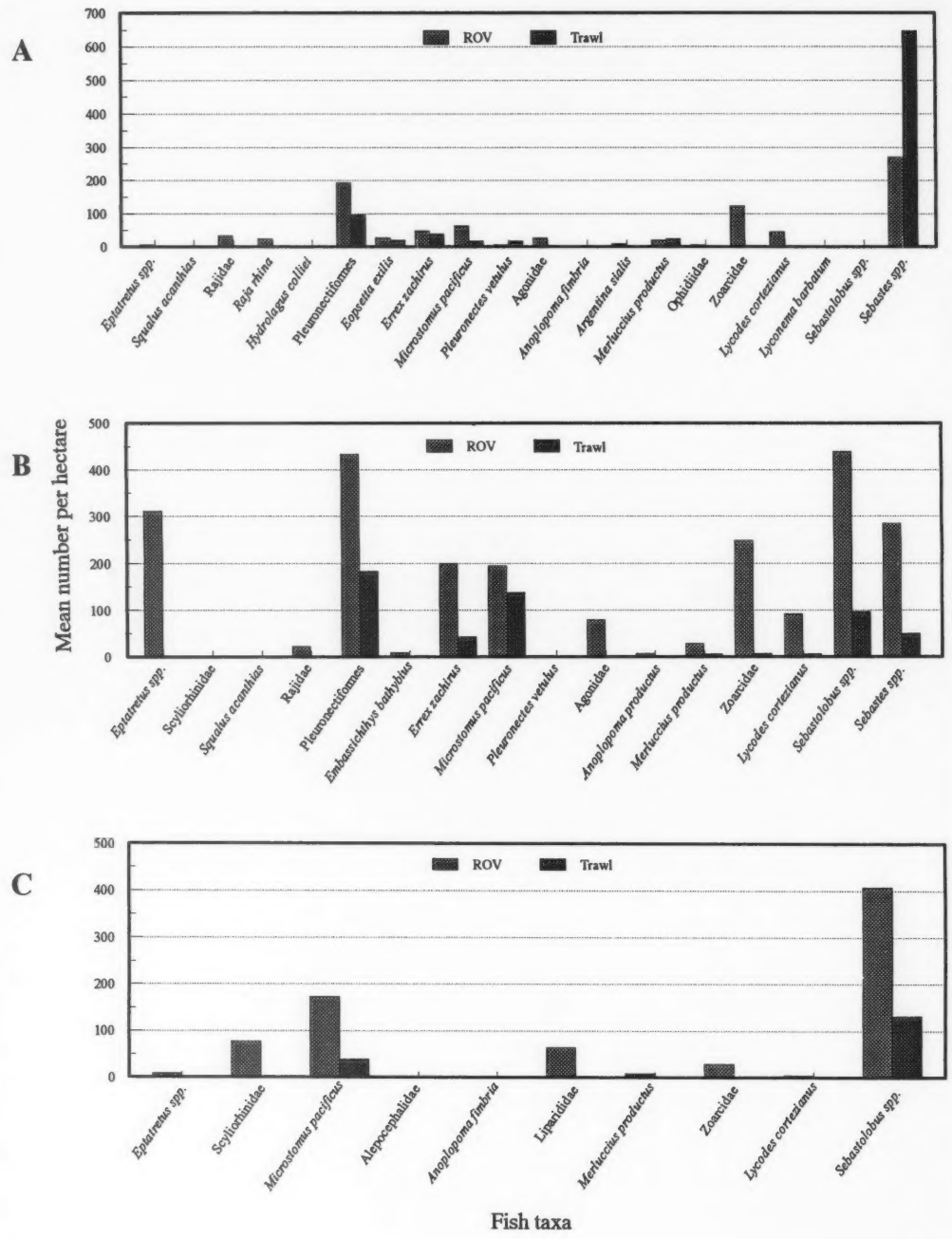

Figure 3

Mean numbers of fish per hectare estimated from an ROV video strip-transect survey and a swept-area trawl survey from (**A**) the 200-m depth station (ROV, n=3 and trawl, n=8); (**B**) the 400-m depth station (ROV, n=4 and trawl, n=8); and (**C**) the 600-m depth station (ROV, n=3 and trawl, n=9).

any abundance (greater than 1 fish/hectare in either estimate). For the 200-m, 400-m, and 600-m depths (Fig. 3), the mean ROV estimates were higher than the trawl estimates for 13 of 20, 15 of 16, and 9 of 10 comparisons, respectively (sign test 200 m: P=0.180; 400 m: P=0.001; and 600 m: P=0.011).

Especially large differences between the ROV and trawl estimates existed for strongly bottom-associated groups: skates, flatfish (Pleuronectiformes), and thornyheads, and particularly for small, cylindrically shaped fish that remained on the bottom: hagfish (*Eptatretus* spp.) poachers (Agonidae), and eelpouts. No significant differences were found between ROV and trawl estimates for fishes with more off-bottom behavior ("roundfish"), such as Pacific whiting, *Merluccius productus*, sablefish, and rockfish. Spiny dogfish, *Squalus acanthias,* were captured at every depth in low numbers in the trawls and were the only species to occur consistently in the trawls that were not seen with the ROV.

Coefficients of variation were generally smaller for the ROV estimates than for the trawl estimates. For species that occurred in both the ROV and the trawls, the coefficients were smaller for the ROV estimate in 10 of 15 comparisons at the 200-m depth, in 10 of 13 comparisons at the 400-m depth, and in 8 of 10 comparisons at the 600-m depth ([Fig. 4] sign test; 200 m: P=0.170; 400 m: P=0.050; and 600 m: P=0.050). ROV coefficients of variation were always larger for catsharks only and were mixed for Pacific whiting and some species of flatfish. At all depths, ROV coefficients of variation were smaller for rockfish and thornyheads, species typically with very large variances. Coefficients of variation for total fish number were much larger for the trawl estimates than for the ROV estimates at all depths (200-m, 2.4 times; 400-m, 4.6 times; and 600-m depths, 3.0 times).

The required sample sizes to detect a 50% reduction in the log-transformed means for a fixed level of power (1–β, 0.80) were smaller for the ROV than for the trawl, except for catsharks (Table 2). When the ROV sample sizes were smaller, the difference in sample sizes ranged from 1.3 to 19 times. For catsharks, a taxon with high variability, the ROV sample size was nearly six times larger than that for the trawls.

Most fishes showed no response to the ROV (Table 3). Considering all fish taxa observed, 80% showed no response to the ROV, 6% were attracted, and 14%

Table 2

The required sample size to detect a 50% reduction from the log-transform mean abundance of commercially important and abundant fish taxa at the 400-m depth from ROV and trawl surveys. The calculations were made at a fixed level of α (0.05) and power (1–β, 0.80).

	ROV	Trawl
Commercially important taxa		
Microstomus pacificus	5	95
Anoplopoma fimbria	25	55
Sebastolobus spp.	29	38
Abundant taxa		
Scyliorhinidae	251	43
Rajidae	9	104
Zoarcidae	14	90

Table 3

Response of commonly occurring fish taxa to the remotely operated vehicle (ROV). Fish from all depths (n=10) were recorded. Unid. = unidentified.

	Strongly attracted	Weakly attracted	No response	Weakly avoided	Strongly avoided
Eptatretus spp.	0	8	182	5	9
Scyliorhinidae	0	2	22	19	0
Rajidae unid.	0	2	42	4	8
Errex zachirus	0	1	89	3	26
Microstomus pacificus	0	3	326	10	21
Anoplopoma fimbria	0	4	5	2	2
Merluccius productus	0	45	28	11	7
Lycodes cortezianus	0	1	69	12	8
Sebastolobus spp.	0	2	173	8	10
Sebastes spp.	0	0	14	2	0
All taxa	0	68	950	76	91

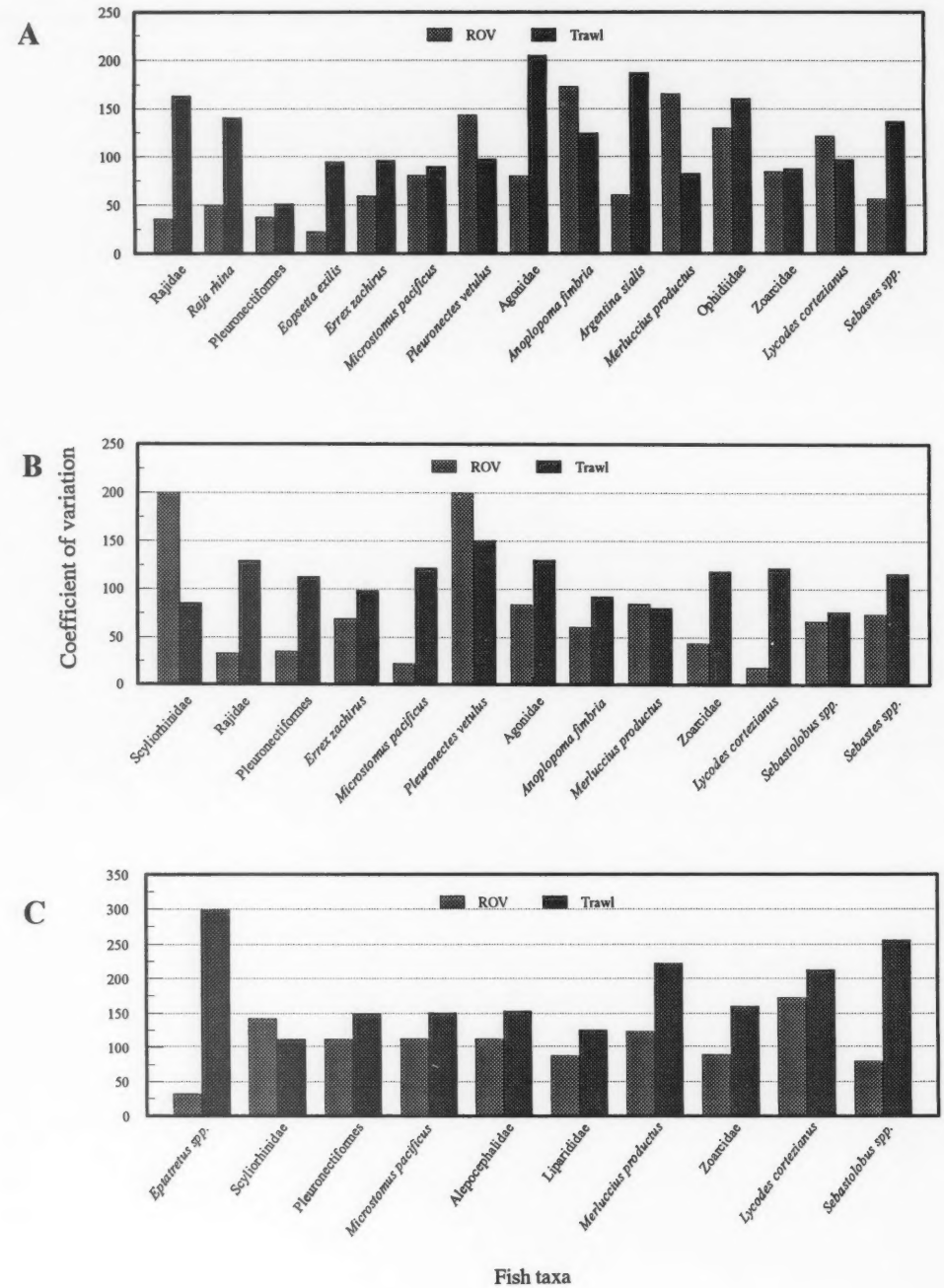

Figure 4

Coefficients of variation of the mean number of fish per hectare estimated from an ROV video strip-transect survey and a swept-area trawl survey from (**A**) the 200-m depth station (ROV, n=3 and trawl, n=8); (**B**) the 400-m depth station (ROV, n=4 and trawl, n=8); and (**C**) the 600-m depth station (ROV, n=3 and trawl, n=9).

avoided it. Pacific whiting had the strongest response (69%), appearing to be attracted to the ROV. Sablefish had the next strongest response (62%), but their numbers were low, averaging 3.75 individuals over all depths. Their behavior was variable: some animals swam away, some swam toward the ROV, and some ignored the ROV. Catsharks showed approximately equal numbers responding and not responding, and those that did respond consistently avoided the ROV.

Finally, the red octopus, *Octopus rubescens*, was the most abundant animal counted from the ROV. It was observed from the ROV only at the 200-m depth at numbers of 1,610 per hectare (SE=516.4) and was not captured in the trawls. The ROV red octopus abundance estimates were higher than any fish estimate from the trawls.

Discussion

Much of the difference between the ROV and trawl estimates was due to the different mechanical nature of the sampling gear and to the body shape and behavior of the fishes. The ROV intensively sampled a narrow area directly in front and extending up a short height off the bottom. The trawl sampled a much wider area, including a larger area off the bottom, but with what must have been a great deal of escapement. The result was that ROV abundance estimates were higher and had lower coefficients of variation for fishes either strongly associated with the bottom or with a body shape and size, or both, that would pass through the mesh (such as the red octopus). Conversely, animals with highly patchy distributions and off-bottom behavior (catsharks, rockfish at the 200-m depth) had higher abundance estimates from the larger volume trawl. Although both the ROV and trawl estimates were adjusted to the same surface area, there was no adjustment made to reflect the 7.7 times greater off-bottom height sampled by the trawl (Fig. 2). Probably neither method does a particularly good job of estimating off-bottom fishes that are patchily distributed. Visual estimates of fish abundance either from submersibles (Uzmann et al., 1977) or from divers (Kulbicki and Wantiez, 1990) are reported to be higher than those from otter trawl estimates for multispecies assessments, but the reverse was true in this study for rockfishes (see also Krieger, 1993).

The smaller sample sizes required to detect a 50% reduction of the ROV abundance estimates would improve the ability to detect trends in abundance such that a smaller increment of change would be detectable. The degree on improvement would vary with species. Reductions of the order of 1.3 to 19 times in required sample size are sufficient to increase the ability to detect true changes in population size. Much of the decrease in required sample size (and increase in statistical power) comes from the much higher ROV abundance estimates. If samples are drawn from two populations with similar levels of variation, a 50% decrease in abundance of the larger estimate is much larger and therefore easier to detect. Unfortunately, a great deal of variation due to patchiness in fish distribution remains.

For an environmental assessment, the ROV estimates provide a better overall picture of the community than do the trawl estimates. While the similarity in the presence and absence of species in the two methods was surprisingly high, the ROV abundance estimates generally tended to be higher and had lower coefficients of variation. Species that were usually in direct contact with the bottom had much higher ROV abundance estimates than did those captured in the trawl. Small, cylindrically shaped fishes (hagfish, poachers, and eelpouts) had particularly large differences between ROV and trawl abundance estimates, probably owing to escapement under the footrope or through the trawl webbing. The most obvious example of escapement or avoidance was that provided by the red octopus, which was more abundant in the ROV sampling than any fish, but which was not captured by the trawl.

For the commercially important species at these depths (Dover sole, thornyheads, and sablefish), the results were mixed. For Dover sole and thornyheads, ROV abundance estimates were higher and coefficients of variation were lower. For sablefish, abudance estimates were higher for the trawl sampling at 200-m and 600-m depths. Although rockfish at the 200-m depth are not commercially important, the trawl estimates for this taxon were higher, and this is likely to be true of commercially important rockfishes.

Stock assessment integrates patterns of removals and information on year-to-year variation in recruitment from catch-at-age data with mean levels of abundance and longer term trends from survey data (Deriso et al., 1985; Methot, 1990). Using simulations, Kimura (1989) showed that, if survey data are biased, the results can be a precise, but biased, inference regarding the population. The higher ROV abundance estimates mean that trawl estimates are biased too low and that there is actually a larger difference between years of low population size and threshold levels of overfishing set by these assessments. The risk of overfishing is actually lower than that which was assumed. A more dangerous situation arises when bottom trawl estimates are larger than the ROV estimates, as with rockfish (also see Krieger, 1993). Here the difference between years of

low population and threshold levels of overfishing is actually less than that which was realized, a difference that increases the risk of overfishing.

ROV's have the ability to identify the degree of species' attraction to or avoidance of the sampling gear. Three species showed a strong response to the ROV: Pacific whiting, sablefish, and catsharks. Pacific whiting was the only species that was attracted to the ROV (Table 3). These three species are usually observed off-bottom and in motion, rather than resting in contact with the bottom. Fishes that are commonly in motion should be in a better position to respond quickly to stimuli (motion, light, etc.) around them. Understanding and accounting for fish behavior could improve the accuracy of an estimate. For trawl gear, the level of attraction or avoidance is unknown. Anecdotal evidence for attraction (crowding of fish between doors suggested by Krieger [1993]) and for avoidance (net sounder readings of rockfish rising up out of the path of the net [Adams[3]]), have been reported, but there is no simple way of evaluating these phenomena for trawl gear.

While the presence of large seasonal or interannual variation in fish numbers could have introduced bias into the estimates, there is no reason to believe this occurred. None of the 20 most common species captured by the three trawl surveys, which covered almost the entire study period, exhibited a consistent seasonal or overall trend in fish abundance. Also, the consistency of trends in abundance derived from ROV's and trawls from all depths, even though they were sampled at different times, suggests that large varations in abundance were not an important source of bias. However, if this bias had occurred, it would have been a larger problem for the ROV estimates than for the trawl estimates. The ROV samples at depth were taken during one time period, with the exception of the 400-m depth, whereas the trawl samples were taken at all depths during three cruises over nearly the entire time period.

Both ROV and trawl surveys contain additional information that may be critical to the goals of an abundance study. ROV surveys provide much biological information, particularly on habitat and species association. In two instances, we observed feeding behavior. Trawl surveys deliver the fish on deck; for common types of biological studies, such as ageing or food habits, these specimens are critical. In addition, these specimens enable accurate species identification. Identifcation, however, is expected to become less of a problem as video technology improves.

Finally, there is the chronic problem of the low statistical power of tests of these abundance estimates owing to large, associated variances. Since increasing the sample size is often not practical, the only alternative is to stratify the sampling more effectively rather than simply on the basis of depth. Better stratification can come only from a greater understanding of the biological factors responsible for fish distributions. An adequate understanding would include the association of fish with microhabitat and the biological behavior of fishes that leads to patchiness. Surveys could then be stratified on the basis of areas where fish are occurring at background levels and in large patches. Trawl surveys have been unsuccessful in achieving such separation. Information gained from the ROV could lead to the biological understanding necessary to achieve more efficient stratification designs.

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Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister**

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Abstract.—The impact of predation by staghorn sculpin, *Leptocottus armatus*, on newly settled Dungeness crab, *Cancer magister*, in the Washington coastal estuary of Grays Harbor was studied. Staghorn sculpin are known to be generalist, opportunistic feeders, with relatively high food requirements for estuarine growth during warm summer months. During late spring or early summer, vast numbers of crab megalopae reach the estuary and settle on intertidal flats and in subtidal channels. During the next two months the young-of-the-year (0+) crab population is rapidly reduced by predation, including cannibalism. Crab without appropriate refuge habitat are highly vulnerable to predation by fish, and accordingly survival of young crab is highest in intertidal shell and eelgrass beds. Abundance and summer growth of crab and sculpin within the estuary were documented by monthly trawling surveys (April to August) in 1989. Stomach contents of sculpin were analyzed to characterize the overall summer diet, to note monthly shifts in major prey items within two age classes of sculpin (0+ and 1+), and to contrast sculpin prey consumed in eelgrass with that consumed in shell habitats. The predominant prey species varied across the categories above but generally included ghost and blue mud shrimp, *Neotrypaea californiensis* and *Upogebia pugettensis*, a nereid polychaete (*Nereis brandti*), juvenile Dungeness crab, *Cancer magister*, and sand shrimp (*Crangon* spp.). Some combination of these species composed 85% of the total diet (on the basis of percentage of total Index of Relative Importance; %IRI) across time and between habitats. A comparison of diets of sculpin collected at eelgrass and shell habitats was significantly different; a strong preponderence of 0+ crab were consumed at the shell habitat. *Nereis brandti* was the most important prey for 0+ sculpin, whereas *Neotrypaea californiensis* was the most important for 1+ and older sculpin. The importance of shell as refuge habitat for *C. magister* and the apparent contradiction in the observation that a large number of 0+ crab were taken by sculpin at the shell habitat are discussed.

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Fishery Bulletin 93:456–470 (1995).

Staghorn sculpin, *Leptocottus armatus*, are common in major estuaries throughout their range from Baja California through the Gulf of Alaska (Hart, 1974). Young sculpin inhabit brackish water streams and channels and move down into the estuary as they grow larger during their first year. Older juvenile and adult sculpin are broadly distributed throughout estuarine nursery areas utilized by juvenile crab and are known predators of Dungeness crab, *Cancer magister*, within estuaries (Reilly, 1983). Staghorn sculpin have wide gapes and relatively large mouth areas in relation to their size compared with other species of fish predators commonly found in estuaries during the summer.[1,2] They are opportunistic, generalist predators (Jones, 1962; Hart, 1974; Birtwell et al., 1984) and feed heavily on decapod crustaceans such as the yellow shore crab, *Hemigrapsus oregonensis*, the ghost shrimp *Neotrypaea californiensis*, and pea crab, *Pinnixa* sp. (Tasto, 1975; Posey, 1986). Staghorn sculpin are described as visual predators that move onto estuarine tideflats with the incoming tide (Tasto, 1975); their foraging behavior may contribute to the high mortality rate of small 0+ crab (Wainwright et al., 1992).

The Grays Harbor estuary, Washington, contains extensive intertidal tracts of eelgrass and shell that serve as critical nursery areas for young-of-the-year (0+) and one-year-old (1+) Dungeness crab[3] (Gutermuth and Armstrong, 1989; Gunderson et al., 1990; Jamieson and Armstrong, 1991). During high tides in May and June, vast numbers of crab megalopae reach estuaries, settle to the benthos, and metamorphose to the first juvenile instar (J1). Crab settle over broad expanses of the intertidal sandflats

* Contribution 903 of the University of Washington, School of Fisheries, Seattle, WA 98195.

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and in subtidal channels but within a few weeks can be found only in areas that afford some refuge[4] (Dumbauld et al., 1993; Fernandez et al., 1993a). First year survival, based on five years of trawl survey data in the estuary (Gunderson et al., 1990), has been estimated at approximately 8% (Wainwright et al., 1992). Different assemblages of predators affect survival of Dungeness crab during each phase of their life history (Reilly, 1983; Stevens and Armstrong, 1985; Thomas, 1985). Estuarine and nearshore fishes, wading birds, and older crab are known to prey upon the young crab instars (Stevens et al., 1982; Fernandez et al., 1993b), causing high mortality rates in the summer months (Wainwright et al., 1992).

Predation, including cannibalism, is considered to be the prime cause of the rapid decline in crab abundance through the summer. Stevens et al. (1982) showed that during years of high 1+ crab abundance, cannibalism can account for a significant portion of 0+ crab mortality. Even early settling 0+ crab are capable of cannibalizing later settlers of the same year class (Fernandez et al., 1993b). However, aside from Reilly's study (1983) in California estuaries, predation by estuarine fish and wading birds has received little attention as a source of crab mortality. Although sea birds are known to take a toll on megalopae[5] and on newly settled crab (Mace, 1983), fish and crab predators are more likely to exert the greatest predation pressure on the highly abundant, small instars during settlement and early development.

In this study, we discuss the estuarine summer feeding patterns of staghorn sculpin with respect to a broad spectrum of crustacean prey but focus on their possible significance as predators of 0+ *C. magister* and on the role of refuge habitat on the basis of spatial patterns of predation in the estuary. A temporal shift in consumption of certain prey taxa is also discussed as indicative of opportunistic feeding by staghorn sculpins with seasonal patterns of prey abundance or with life history events which make prey more susceptible to predators.

Materials and methods

Sampling scheme

Grays Harbor (46°55'N, 124°05'W) is a major Washington coastal estuary of about 8,545 hectares (Gunderson et al., 1988) marked by numerous subtidal channels. These channels extend across extensive sandflats that become exposed and represent 67% of surface area during spring low tides. Refuge habitat is provided by epibenthic shell exposed from remnant *Mya arenaria* and *Crassostrea gigas* bivalve populations and by eelgrass. Shell coverage has been calculated to account for 19% of the total intertidal area,[6] whereas eelgrass (*Zostera marina* and *Z. noltii*) was reported to cover 42% of the tidal flat area.[7]

Staghorn sculpin were collected from Grays Harbor during six sampling trips from April through August 1989. Sampling was timed to coincide with the following periods: April–May prior to the main pulse of annual crab settlement, June (two trips) during recruitment of 0+ crab, and July–August during the post-settlement summer growth period. Two intertidal sandflat sites located about 10 km apart were routinely trawled at high tide as a means of contrasting diet in two common epibenthic habitats of the estuary: an eelgrass (*Zostera* spp.) bed in North Bay, and shell piles (*Mya arenaria*) in South Channel (Fig. 1). In order to ensure reasonable sample sizes of fish for each trip and site (target of $n>20$), two trawls each were conducted at both an intertidal station (during slack flood tide) and at an adjacent subtidal station (at low slack) within 6 h on the same day, and fish were pooled for analyses of differences in diet over time. Additional subtidal trawls were made as time permitted for a total of 9–11 trawls per trip.

All trawl samples were collected with a 3-m beam trawl (Gunderson and Ellis, 1986) deployed from a 7-m Boston Whaler. The net had an effective fishing width of 2.3 m and a 4-mm codend liner to retain juvenile crab and fish. Trawls in subtidal channels were run for about four minutes at a speed of 3.7 to 5.6 km/h. Distance fished was determined by optical range finder fixes between buoys deployed at the beginning and end of each tow (see Gunderson et al., 1990, for details of trawl procedure); such distances ranged from 200 to 350 m. Intertidal tows were made between two staked points 160 m apart. Distance fished and fishing width of net were used to estimate area swept for calculation of catch per unit of effort (CPUE; number per hectare). Trawl contents were characterized as to type of vegetation (e.g. algae,

[4] Armstrong, D. A., L. Botsford, and G. S. Jamieson. 1990. Ecology and population dynamics of juvenile Dungeness crab in Grays Harbor estuary and adjacent nearshore waters of the southern Washington coast. Rep. to U.S. Army Corps of Engineers, Seattle District, Seattle, WA, 140 p.

[5] Armstrong, D. Personal observation at Whitcomb Flats sea gull nesting site, Grays Harbor, WA, May 1988.

[6] Dumbauld, B. R., and D. A. Armstrong. 1987. Potential mitigation of juvenile Dungeness crab loss during dredging through enhancement of intertidal shell habitat in Grays Harbor, Washington. Final Rep. FRI-UW-8714 to U.S. Army Corps of Engineers, 64 p.

[7] Smith, J., L. D. R. Mudd, and L. W. Messmer. 1977. Impact of dredging on the vegetation in Grays Harbor. Appendix F *in* Maintenance of dredging and the environment of Grays Harbor, Washington. Final Rep. by U.S. Army Corps of Engineers, Seattle District, 94 p.

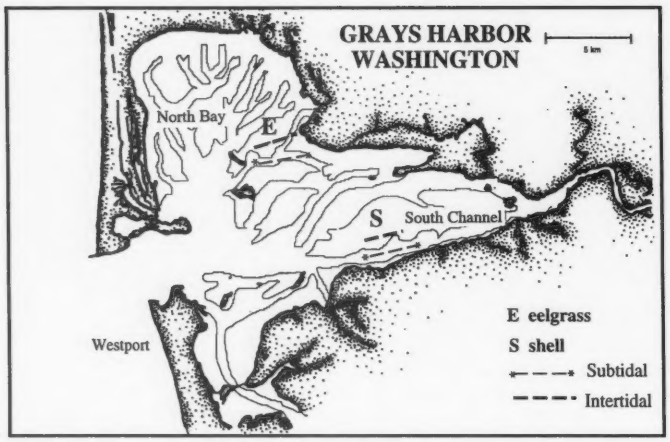


Figure 1

Grays Harbor, Washington, sampling locations for staghorn sculpin, *Leptocottus armatus*, and Dungeness crab, *Cancer magister*, at eelgrass (E) and shell (S) sampling sites. Bold dashed line denotes intertidal trawls and lighter dashed line indicates subtidal channel trawls.

eelgrass, terrestrial leaves), shell, and underlying substrate. All fish and crab were sorted from the catch, identified to species, and counted. Crab were measured (carapace width [CW] inside the 10th lateral spine), sexed, and returned to the water. Staghorn sculpin were picked from the catch and killed. Their body wall was slit, and the fish were preserved in 10% formalin in sea water and later transferred to 70% ethanol in the lab for measurement (total length, TL) and stomach content analyses.

Length-frequency data for sculpin and crab were used to determine instar and year-class composition. Crab length-frequency histograms by trip were used to establish the presence of the 1989 year class of 0+ crab from first tentative appearance in May, at peak settlement in early June, and at the time of summer growth through August. Size modes for crab instars (juvenile crab 6–40 mm CW) were visually determined from length-frequency histograms (hereafter crab instars 1 through 7 will be referred to as J1–J7 and conform to instar sizes specified by Wainwright and Armstrong [1993] and Dinnel et al. [1993]). Evaluation of size ranges and modes as compared with stage (CW for crab; TL for sculpin, Tasto, 1975) were used to set the upper size limits for 0+ and 1+ age classes each month during the summer.

Sculpin gape measurements

Sculpin mouth widths (measured for 466 sculpin) were used as an index of mouth gape size. The mouth of a preserved specimen was gently pried open as far as possible and the internal distance from the intersections of upper and lower jaws was measured. Since fish body lengths are more commonly reported as standard lengths (SL), sculpin total lengths (TL) were converted to standard length for a discussion of mouth gape to body length relationship[8]:

$$SL = 0.87338\ TL - 2.7584$$
$$(r^2 = 0.995, n = 53).$$

Stomach content analyses

Stomach contents of all staghorn sculpin from a trawl were examined up to a total of 20 fish. When catches were higher, the fish were separated into 5-mm size intervals, then proportionally subsampled until a total of 20 fish were selected for stomach analyses. Sculpin were measured (TL), blotted on paper towels, and weighed wet to the nearest 0.1 g. Then their stomachs were removed, blotted, and weighed with and without contents to derive stomach content weight. An estimate of relative stomach fullness was derived by using six categories corresponding to empty, 1/4, 1/2, 3/4 full, full, and "distended." In the latter case, quantity of prey within the stomach resulted in pronounced distention of the body wall beyond the normal lines and curvature of the fish. Sculpin stomachs were analyzed to document the frequency of occurrence of Dungeness crab, the overall proportion of the diet attributed to major prey categories, and the relationship between sculpin size and size of juvenile crab prey.

Food items were generally identified to species unless obscured by digestion. Prey species consumed frequently were analyzed as a distinct prey category, but species that were consumed infrequently were combined to form a more general prey taxon that also included prey items obscurred by digestion. As an example, the amphipod *Eogammarus confervicola* was recorded as a separate prey category owing to its high frequency of occurrence, but several species of fishes (*Gasterosteus aculeatus*, *Lumpenus sagitta*, *Cymatogaster aggregata*, *Leptocottus armatus*, *Pleuronectes vetulus*, and *Citharichthys* sp.) were consumed infrequently and were thus grouped as "fish." Analysis of stomach content data was done by

[8] Williams, G. Pacific Estuarine Research Labs., San Diego State Univ., San Diego, CA. Unpubl. data, 1991.

calculation of a modified form (Stevens et al., 1982) of the Index of Relative Importance (IRI) (Pinkas et al., 1971; Hyslop, 1980) based on estimated food weight rather than food volume. For a particular prey category, an IRI value was calculated as

$$IRI = (NC + GC)FO,$$

where *NC* (numerical composition) is the number of a particular prey item divided by the total number of all prey items in that sample multiplied by 100, *GC* (gravimetric composition) is the combined weight of a particular prey item divided by the total weight of all stomach contents in the sample multiplied by 100, and *FO* (frequency of occurrence) is the number of stomachs from a sample containing a given prey item divided by the total number of fish sampled multiplied by 100. IRI values from all prey categories were summed to derive a grand total IRI value. The relative importance of each prey category was then expressed as a percentage of this total IRI (hereafter referred to as %IRI).

Data analysis

Sculpin stomach content data were analyzed from four perspectives. First, an overall summer diet for staghorn sculpin was derived by combining all fish from both sites (E and S), inter- and subtidal, across months to determine dominant prey taxa. Second, a temporal comparison of sculpin diets from late spring through summer was made by examination of sculpin stomachs grouped by sampling trip. Third, the effect of sculpin size (and thus age) on diet was investigated for two size groupings derived from length-frequency histograms of sculpin caught during the six trips. Size ranges and age equivalents were set from the literature (Anaheim Bay, CA, [Tasto, 1975]; Yaquina Bay, OR [Bayer, 1985]) to group fish by age class as either 0+ (n=210) or ≥1+ (n=256). IRI analyses were run separately on 0+ and ≥1+ sculpin to determine whether there were changes in diet composition based on predator size. Fourth, prey composition of sculpins feeding at different epibenthic habitats was compared by examining diets of fish collected from the intertidal eelgrass site (n=55) and diet of sculpin caught at the intertidal shell site (n=44).

To compare dietary overlap of sculpin of the two size/age categories or of sculpin collected at the two different habitats (eelgrass vs. shell), Schoener's (1970) index of overlap (S_{IO}) was calculated as

$$S_{IO} = 1 - 0.5\left(\sum_{j=1}^{n}\left|P_{x_i} - P_{y_i}\right|\right),$$

where P_{xi} = the proportion of prey i (%IRI) in the diet of sculpin of size x (or from habitat x);
P_{yi} = the proportion of prey i (%IRI) in the diet of sculpin of size y (or from habitat y),
and j = the number of prey types. An overlap value of $S_{IO} \geq 0.6$ (Schoener, 1970) was considered significant in this study.

Results

Overall summer diet

A total of 482 staghorn sculpin stomachs were collected from April to August 1989, of which 458 had some stomach contents. Sculpins averaged 118 mm TL (range: 61–215 mm TL) during the five-month sampling period (Table 1). Mouth gape width ranged from 13 to 17% of standard length (gape width = 0.1818 SL–2.6487, r^2=0.909; Fig. 2). Average fish length and weight varied by sampling month and were generally greater in April and May when samples were composed primarily of 1+ fish, decreased in June as 0+ sculpin moved into the sampling sites, and increased in July and August as individuals grew through summer (Fig. 3; Table 1). Size-frequency data indicated the presence of two modes equivalent to 0+ and 1+ age classes. Young of the year ranged from 60 to 94 mm TL in April and had grown to 75–119 mm by August (Fig. 3). For purposes of analyses of diet based on size-age composition of sculpin, 118 mm TL was used as the boundary between 0+ and 1+ groups. These size-age categories were corroborated by otolith annuli determinations of a similar size range of staghorn sculpins from Vancouver Island, British Columbia, estuaries by Mace (1983, p. 369).

The mean number of individual prey items per sculpin was 3.4, and gut fullness was generally high; 75% of all stomachs examined were rated 50% full or greater whereas fewer than 5% were empty (Fig. 4). Sculpin stomach contents included 23 prey taxa (Armstrong, 1991) which were grouped into 14 prey categories for IRI analyses (Table 2). Principal categories of sculpins' overall summer diet (% IRI) were the polychaete *Nereis (Neanthes) brandti* (30% IRI), the ghost shrimp *Neotrypaea californiensis* (27% IRI), sand shrimps *Crangon* spp. (13% IRI, including *C. franciscorum*, *C. nigracauda*, and *C. stylirostris*), juvenile *Cancer magister* (9% IRI), and the mud shrimp *Upogebia pugettensis* (6% IRI).

Temporal changes in diet

Stomach contents were analyzed on a per trip basis to note change in sculpin diet over the course of the

Table 1

Summary data for groups of staghorn sculpin, *Leptocottus armatus*, sampled during monthly trips and for all sculpin combined from April to August 1989 from Grays Harbor, Washington, for stomach content analysis. During each trip all sculpin were caught from both sites, eelgrass and shell habitats, inter- and subtidal trawls combined. SD = 1 standard deviation, TL = total length.

	Fish size (mm TL)			Fish wet wt. (g)			Mean gape			
Dates	Mean	1 SD	Range	Mean	1 SD	Range	(mm)	No. stomachs examined	% empty	Mean no. prey per sculpin
Apr 7–8	113	21	(61–190)	17	11	(2–70)	14.8	111	0	7.1
May 6–7	138	27	(94–215)	36	28	(9–133)	18.9	38	3	2.5
Jun 4–6	108	25	(72–173)	17	14	(3–62)	14.7	62	0	2.7
Jun 18–19	99	19	(70–162)	12	9	(4–55)	12.2	126	4	2.3
Jul 19–20	121	23	(78–169)	21	13	(4–53)	16	61	11	1.4
Aug 15–18	127	28	(84–213)	24	19	(6–102)	16.7	84	8	3.3
Combined grand mean	118	27	(61–215)	20	17	(2–133)	15.6	482	5	3.4

summer. Entry of small sculpin into our sampling areas in June was inferred by the decrease in mean sculpin size and wet weight (Table 1) and supported by examination of length-frequency histograms (Fig. 3).

Diet composition changed appreciably from month to month. During the spring, sculpin primarily consumed the gammarid amphipod *E. confervicola* (46% IRI), *Crangon* spp. shrimp (24% IRI), and fish (13% IRI) in April (Fig. 5), whereas the nereid polychaete *N. brandti* (34% IRI), the thalassinid shrimps *N. californiensis* (45% IRI), and *U. pugettensis* (12% IRI) were the most abundant prey in stomachs in May (Fig. 5). Sculpin consumed few crab, reflecting the relative scarcity of 0+ instars in late spring; J1 instars were found in only 5% of sculpin stomachs in May and represented less than 1% IRI. Minimal settlement of Dungeness crab during May was indicated by low catches of 0+ crabs (Fig. 6; only three J1 were caught in 10 trawls).

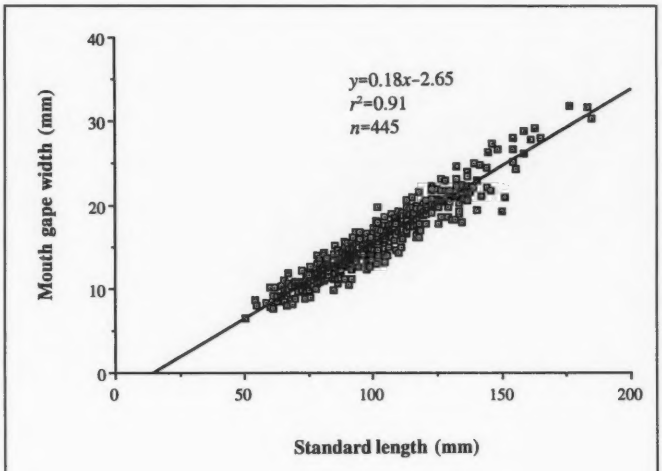


Figure 2

Staghorn sculpin, *Leptocottus armatus*, mouth gape width (y) to standard body length (x) relation based on 445 sculpin from Grays Harbor, Washington, April–August 1989.

In early June, juvenile Dungeness crab recruited to the estuary (Fig. 6) and became the second most important diet category (24% IRI, Fig. 5). The nereid polychaete *N. brandti* was first in dietary importance, accounting for 59% IRI, and *Crangon* spp. shrimp ranked third (10% IRI) in early June. The major pulse of 0+ crab settlement had occurred during late May–early June (after the mid-May sampling; Fig. 6) and thus J1 and J2 crab had become readily available prey by the beginning of summer. Nereid polychaetes continued as the most important prey item through mid-June (88% IRI), whereas *C. magister* juveniles accounted for only 4% IRI and were consumed by 24% of the sculpin examined.

During the mid and later part of summer, decapod crustaceans represented the majority of staghorn sculpin diet. In July and August nereid worms were rarely found in stomach contents, but thalassinid shrimp, *N. californiensis* and *U. pugettensis*, together totalled 70% IRI in July and 54% IRI in August (Fig. 5). Juvenile crab accounted for 15% and 13% IRI of

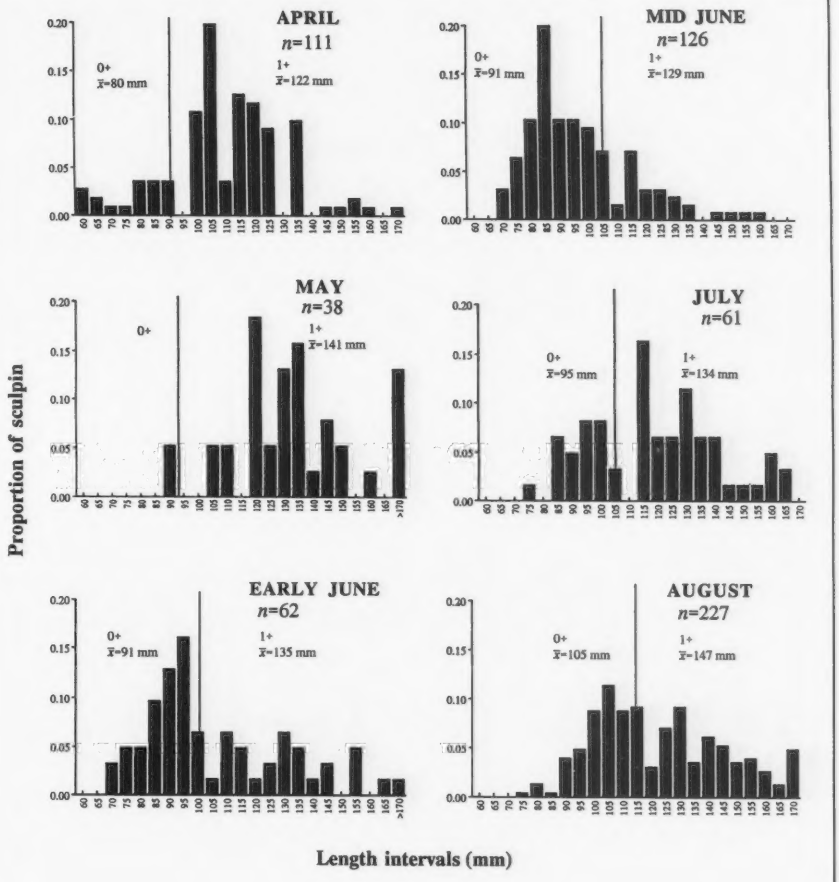


Figure 3

Staghorn sculpin, *Leptocottus armatus*, length-frequency histograms and inferred age classes (0+ and 1+ and older) from Grays Harbor, Washington, April–August 1989. Vertical line indicates upper size cut-off of 0+ from 1+ sculpin. Mean sizes of the age class are given by $\bar{x}$, n = total number of fish examined, both age classes combined.

sculpin diets during these months and *Crangon* spp. for 10% and 11% IRI.

Sculpin age-class and prey composition

Sculpin length-frequency histograms by trip were examined and fish were separated into two age groups based on size (Fig. 3). The diets of 0+ and ≥1+ sculpin were compared to determine whether there were differences in prey composition based on fish size. Both sculpin age groups had the same proportion of empty stomachs (5%) and the same mean number of prey species (3.4) per predator, indicating similar feeding success rates. Small (0+) sculpins primarily consumed *N. brandti* (50% IRI), *N. californiensis* (13% IRI), *Crangon* spp. (11% IRI), *C. magister* (9% IRI), bivalve siphon tips, and miscellaneous or unidentified crustaceans (5% IRI each; Fig. 7). Larger sculpins consumed less *N. brandti* and crangonid shrimp (23% and 5% IRI) but more thalassinid shrimp (*N. californiensis* [31% IRI] and *U. pugettensis* [12% IRI]) and large gammarid amphipods (*E. confervicola* [8% IRI]). Dietary overlap was significant (S_{IO}=0.6). Sculpins over the entire size range sampled (70–215 mm TL) consumed young Dungeness crab (9% of IRI in the summer diet of both

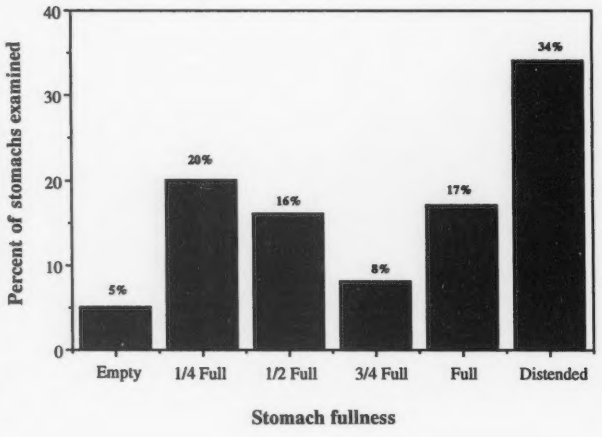


Figure 4

Relative-frequency histogram of staghorn sculpin, *Leptocottus armatus*, stomach fullness. All sculpin (n=482) from Grays Harbor, Washington, April–August 1989.

Table 2

Summer diet composition of staghorn sculpin, *Leptocottus armatus*, from Grays Harbor, Washington, all data combined, April–August 1989. Values are percent composition by number (%NC), weight (%GC), frequency of occurrence (%FO), and percent of total Index of Relative Importance (%IRI) by prey categories. Bold values indicate the five most important prey categories as measured by % total IRI. The total cumulative percentage of the diet comprised by those five categories appears in the bottom line of the table.

Prey category	%NC	%GC	%FO	%IRI
Nereis brandti	9	30	30	**30**
Neotrypaea californiensis	9	27	30	**27**
Crangon spp.	12	7	27	**13**
Cancer magister	9	7	22	**9**
Upogebia pugettensis	3	17	11	**6**
Eogammarus confervicola	13	<1	12	4
Misc./unid. crustacea	9	2	12	3
Fish	4	6	12	3
Bivalve siphon tips	10	<1	10	2
Misc./unid. amphipods	6	<1	7	1
Allochestes spp.	5	<1	5	<1
Corophium salmonis	6	<1	5	<1
Misc./unid. polychaetes	2	<1	5	<1
Algae	3	<1	8	<1
Total cumulative percentage of diet within top 5 categories				**85% IRI**

0+ and 1+ sculpin). Whole bodies of crab instars, J1–J4 (mean CW: 6–21 mm), were found in sculpin stomachs (Fig. 8).

Habitat comparison

Sculpin diets from two intertidal sites dominated by eelgrass and epibenthic shell (Fig. 1; E and S) were compared. At each site two trawls per trip were made at high tide after sculpin had moved from the adjacent subtidal channels up onto the flats to feed. Mean number of individual prey items per predator (about 3) was the same at both sites, but the percentage of empty guts was significantly lower among sculpin caught over the eelgrass compared with the percentage of empty guts among sculpin caught over shell habitat (2% vs. 11%; approximation of Fisher Exact Test, Z=1.98, P=0.024, Zar, 1984). Mean length of sculpin captured at the eelgrass and shell sites were 104 ±24 mm (1 SD) and 123 ±27 mm TL, respectively. The most pronounced difference in sculpin diets between sites was that juvenile *C. magister* composed 77% IRI over shell habitat but only 5% over eelgrass (Fig. 9). Frequency of occurrence of crab in sculpin stomachs was 3.6 times greater over shell habitat than over eelgrass habitat (69% FO vs. 19% FO). In addition to *C. magister*, the other top diet categories at shell habitat were ranked as *N. californiensis* (7% IRI), *U. pugettensis* (6% IRI), *N. brandti* (5% IRI), and unidentified amphipods (2% IRI). In contrast, primary prey at the eelgrass habitat were *N. californiensis* (27% IRI), *N. brandti* (25% IRI), and *Crangon* spp. (24% IRI). *Cancer magister* and bivalve siphons represented 5% and 4% IRI respectively (Fig. 9). There was not significant dietary overlap in sculpin diets between the two habitats (S_{IO}=0.2).

Staghorn sculpin and 0+ crab densities

Relative density at intertidal and subtidal channels To assess the availability of crab as prey for sculpin predators, relative density was calculated for both sculpin and 0+ crab to contrast intertidal and subtidal eelgrass and shell habitats. At either site, relative crab densities were initially higher on the intertidal compared with adjacent subtidal channels during peak crab settlement in June. Intertidal densities in shell habitat at South Channel were about 9,500/ha in early June and declined to 6,000/ha later in the month. However, in the adjacent subtidal channel crab densities were less than 100/

ha where the primary epibenthic cover is allochthonous leaves, branches, and bark. Initial mean crab densities were almost four times higher in the intertidal shell than at the intertidal eelgrass site (Fig. 10; 9,500 crab/ha vs. 2,500 crab/ha, *t*-test, t=2.4, P=0.136). At the eelgrass site, intertidal and subtidal crab densities were comparable by mid-June at about 2,500/ha. As the summer progressed, 0+ crab density declined in the intertidal at both the shell and eelgrass sites to about 900/ha and 320/ha, respectively, but increased in the subtidal channel adjacent to the shell habitat (Fig.10). The subtidal epibenthos at the shell site in South Channel is composed predominately of wood, bark, and leaves, whereas the subtidal benthic cover at the eelgrass site is primarily shell, eelgrass, and algae; these differences probably contribute to the density differences in mid-June between the two locations.

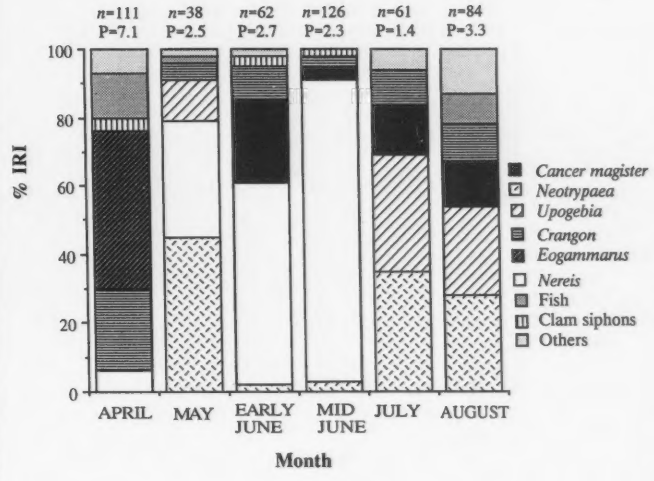


Figure 5

Diet composition of staghorn sculpin, *Leptocottus armatus*, from Grays Harbor, Washington by month, expressed as % IRI. n = number of fish examined and P = mean number prey per predator.

Relative density at shell habitats Sculpin densities at the shell habitat were always higher in the intertidal areas than in the subtidal channel except in mid-June (Fig. 10). In contrast, at the eelgrass site there were higher densities of sculpin in subtidal than in intertidal areas in early June (230 vs. 40 sculpin/ha), but by August higher mean sculpin densities occurred in the intertidal areas (138 vs. 30 sculpin/ha).

Discussion

Importance of crustaceans as prey

Juvenile staghorn sculpins have been reported to feed heavily on small crustaceans including amphipods and isopods. Studies in Tomales Bay, California (Jones, 1962), and the San Juan Islands, Washington (Thornburgh, 1980), have shown that juvenile sculpin primarily consume amphipods, especially *Corophium* spp., mysids, and shrimp. Smith (1980) reported that juvenile staghorn sculpin (20–80 mm TL) in Skagit Bay, Washington, consume the amphipods *Corophium salmonis* and *Anisogammarus confervicolus*, tanaids, and the polychaete *Neanthes limnicola*. Dinnel et al. (1990) showed ontogenetic diet shifts for staghorn sculpin from Padilla Bay, Washington. The smallest sculpin (45–79 mm TL) consumed amphipods and isopods; sculpin 80–119 mm consumed amphipods, isopods, and crabs; and the largest sculpin (≥120 mm) consumed isopods, crabs, and fish. While juvenile sculpin less than 60 mm TL were not sampled in the present study, no significant diet shift was noted for the two size groups (60–119 mm and ≥120 mm) of the Grays Harbor prey assemblage, although relative importance of items differed between the size groups. Smaller fish did consume a relatively higher proportion of polychaetes, whereas larger sculpins consumed more thalassinid shrimp (Fig. 7).

Other studies have shown that adult staghorn sculpins consume crustaceans as a major portion of their diet when they are available. Dinnel et al. (1990) found that amphipods, isopods, and an assemblage of crab species (including *C. magister* and *Pinnixa* spp.) composed a majority (79% IRI) of the August diets of staghorn sculpins from Padilla Bay, Washington. Data presented by Jones (1962) and Boothe (in Tasto, 1975) showed that the majority of staghorn sculpin diet (92% IRI) consisted of decapod crustaceans, including *Crangon* spp., *Upogebia pugettensis*, and a crab assemblage of *Cancer* sp., *Hemigrapsus sp.*, *Pinnixa* sp., and *Scleroplax* sp. Year-round sampling in Anaheim Bay, California, revealed that sculpin consumed primarily decapod crustaceans (78% of the diet by weight) including *N. cali-*

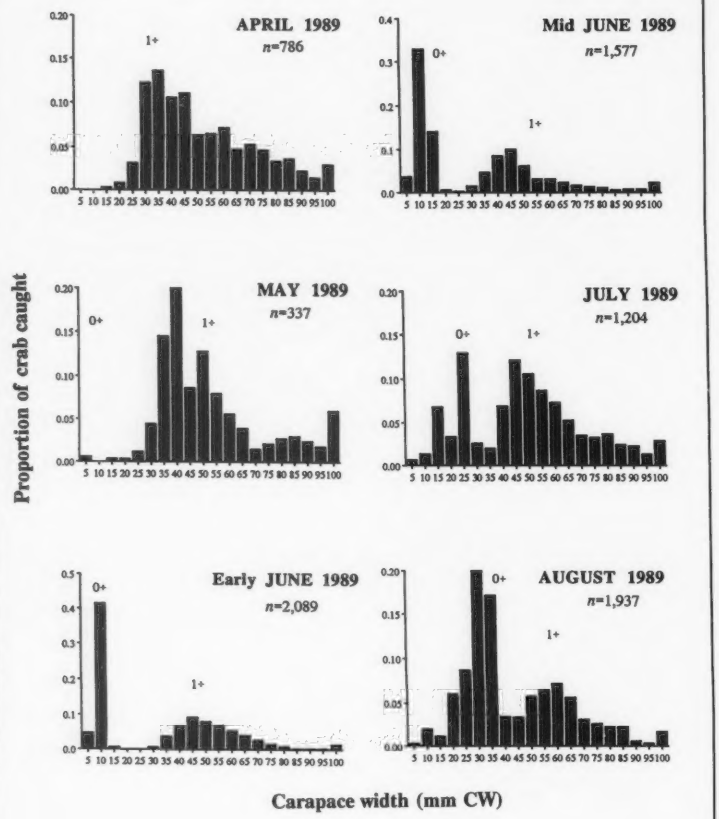


Figure 6

Dungeness crab, *Cancer magister,* length-frequency histograms from Grays Harbor, Washington, April to August 1989. Note first occurrence of 0+ crab in May (6 mm CW) and peak settlement in early June. Summer growth of 0+ crab is evident by 0+ size modes attaining 30–35 mm CW by August.

forniensis, H. oregonensis, and pea crabs, *Pinnixa* spp. (Tasto, 1975). A multi-species assemblage of crab including *Pugettia producta, Cancer productus* and *C. gracilis, Pinnixa* spp., *Scleroplax granulata* (pea crabs), *Hemigrapsus nudus, H. oregonensis,* and *Pagurus* spp. accounted for 25–30% of the spring diet (by volume) of staghorn sculpins >100 mm TL in an estuary of Vancouver Island, British Columbia (Mace, 1983).

The summer diet of staghorn sculpins from Grays Harbor, Washington, corroborates Tasto's (1975) observation that the diet of staghorn sculpin >70 mm TL consists of crustaceans, especially decapods including ghost and mud shrimp (*N. californiensis* and *U. pugettensis*), sand shrimp (*Crangon* spp.), and seasonally abundant 0+ *Cancer magister*. From IRI analysis, it was determined that Dungeness crab represented about 9% of the overall total summer diet of sculpin. Over 30% of all staghorn sculpin collected during June and 23% during July and August had 0+ Dungeness crab in their stomachs. Two other decapods that composed even greater proportions of the overall sculpin summer diet were *Neotrypaea californiensis* and *Crangon* spp. (27% and 13% IRI, respectively).

Other prey

Staghorn sculpin also consume prey species such as nereid polychaetes, fish, and bivalves that are seasonally abundant and readily available (see Gunderson et al., 1990, for list of infaunal and epifaunal prey in Grays Harbor). These sculpin have relatively plastic feeding behavior and their diet changes month to month, fluctuating with relative prey abundance and accessibility. Despite this plasticity, the majority of this species' diet (85–99% IRI) generally consisted of only 4 or 5 prey species (Fig. 5; Table 2). In April, before crab were available, sculpin consumed amphipods, especially *E. confervicola*, and *Crangon* spp. shrimp. Nereid polychaetes and the thallassinid shrimp *Neotrypaea californiensis* were primary prey in May. Dungeness crab were incorporated into the diet as they settled in June and were ranked second in IRI importance after *N. brandti*.

The late spring or early summer predominance of *N. brandti* polychaetes in the diet of sculpin was somewhat unexpected because polychaetes have not often been reported as a major diet item by other researchers from Washington (Smith, 1980; Thornburgh, 1980; Dinnel et al., 1990), or British Columbia (Mace, 1983), although they are mentioned as prey among fish from California (Jones, 1962; Tasto, 1975). The importance of this polychaete during spring and early summer to sculpin in Grays Harbor suggests that adult worm reproductive activity (Bass and Brafield, 1972; Giese and Pearse, 1975; Durchon, 1984) might make them vulnerable to sculpin preda-

tion at this time of year. We examined well-preserved specimens of this polychaete from stomach contents but found all were immature. High predation on immature stages of *N. brandti* may indicate worms are leaving their burrows to disperse as described by Dean (1978). By July and August, the behavior of the polychaetes may have changed, or their abundance may have declined since worms were rarely observed from stomach contents during those months.

Dungeness crab

Predation on 0+ Dungeness crab by sculpin is of interest because of the substantial commercial value of the *C. magister* fishery from northern California through southeast Alaska (Botsford et al., 1989) and because of the ecological implications of this estuarine predator-prey relation that is dependent on the annual arrival of oceanic crab larvae. Estuaries are important nursery grounds for 0+ crab (Cleaver, 1949; Tasto, 1983; Gunderson et al., 1990) and provide refuge by means of several habitats including eelgrass and epibenthic shell (Stevens and Armstrong, 1985; Gunderson et al., 1990; Jamieson and Armstrong, 1991; Dumbauld et al., 1993). Fernandez et al. (1993a) demonstrated that megalopae and newly settled 0+ *C. magister* prefer heavy shell habitat over eelgrass, mud with scattered shell, or bare mud. In addition, field tethering of crab in Grays Harbor showed that shell provided the best protection from predation compared with other habitats and that crab tethered with attached hooks were most often attacked by staghorn sculpin.

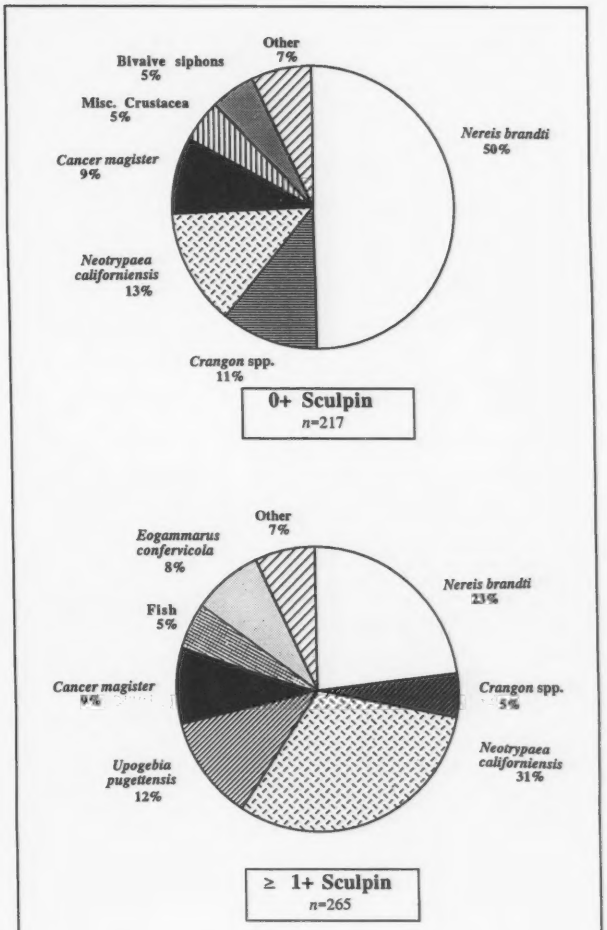


Figure 7

Staghorn sculpin, *Leptocottus armatus*, diet composition from Grays Harbor, Washington, expressed as %IRI, by age class; 0+ and ≥1+ sculpin. All data were combined from April to August 1989.

During peak crab settlement in early June, juvenile crab were found in 42% of the sculpin stomachs examined and represented 10% of the total diet by weight (%GC), or 24% of IRI (Fig. 5). At this time crab are highly vulnerable to predation; the small J1 and J2 instars (6–11 mm CW) are very abundant (over 100/m^2; Fernandez et al., 1993b), compete for limited refuge habitat, and molt frequently (every 2–3 weeks; Wainwright and Armstrong, 1993). The temporal pattern of 0+ intertidal density is consistent with inferences regarding both the rapid predation of much of the 0+ crab population shortly after settlement and with the relative importance of epibenthic shell as a refuge to ensure some survival of the year class. From early June to July, 0+ density decreased an order of magnitude at both the intertidal shell and eelgrass sites as measured by trawl, but density was generally about three times higher over shell habitat compared with eelgrass habitat (Fig. 10). This difference in density between the two habitats is likely much greater than that indicated by the trawl data. Net efficiency is unknown, but the gear was designed to operate on a fairly uniform sand-mud substrate (Gunderson and Ellis, 1986) and, we assume, is less efficient over the shell habitat compared with eelgrass habitat (although much shell is taken in trawls). More importantly, the net "integrates" animals and material along the trawl path and cannot provide distinctions over smaller spatial scales of highly heterogeneous habitat such as intertidal shell. We know from previous intertidal work done in Grays Harbor that

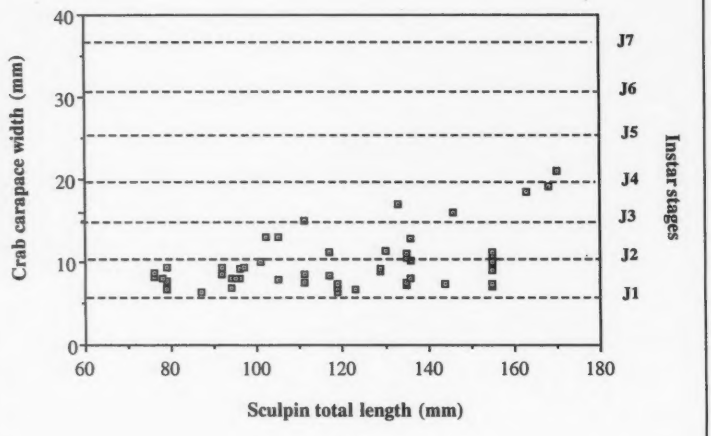


Figure 8

Relationship between body length (TL) of staghorn sculpin, *Leptocottus armatus*, predators and carapace widths of Dungeness crab, *Cancer magister*, instars consumed. Left axis shows mean sizes of instars J1–J7 (dotted lines) from Wainwright and Armstrong (1993).

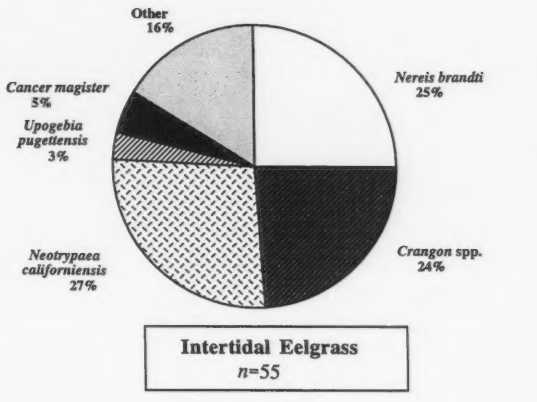
megalopae settle and that J1 instars occur initially on both open tideflats and in refuge materials (e.g. shell, eelgrass) but are absent from the former within several tidal cycles and are virtually never found on open flats thereafter[9] (Dumbauld et al., 1993). Detailed excavation of shell patches at low tide reveal post-settlement densities of J1 in excess of 100/m^2, but only a few per m^2 in eelgrass (Fernandez et al., 1993a), which suggests that trawl data collected at high tide are likely a substantial underestimate of 0+ crab in shell compared with crab in eelgrass.

These observations reflect a paradox indicated by the data. Higher apparent crab consumption was measured among sculpin collected from the shell habitat (77% IRI) than from the eelgrass (5%) (Fig. 9), inconsistent with the notion that shell provides critical refuge habitat for small crab instars. The mean density of 0+ crab from eelgrass intertidal trawl sites decreased by an order of magnitude from 2,455 crab/ha in early June to 280 crab/ha in mid-July (Fig. 10). During the same period, mean 0+ crab density in shell habitat decreased from 9,452 crab/ha to 874 crab/ha, reflecting migration into the channels (Wainwright, 1994) and the impact of predation including cannibalism (1+ on 0+ instars [Stevens et al., 1982]; early 0+ on later 0+ [Fernandez et al. 1993b] fish on 0+ crab [Fernandez et al. 1993a]). There appears to be a short time period during peak crab settlement when staghorn sculpin eat many small instars, especially those that settle on bare sand or mudflats. In this respect Dungeness crab survival throughout much of the bay is dependent upon the availability of suitable refuge habitat[2,10] (Fernandez et al., 1993a) as has been found for juveniles of other decapod species (Herrnkind and Butler, 1986; Barshaw and Lavalli, 1988; Howard, 1988; Warren, 1990).

This pattern may be explained by the short time scale of settlement and rapid predation on small instar crab (especially J1–J2). A possible explanation for the difference in observed crab consumption by sculpin between the two habitats is that crab settlement in eelgrass or on open tideflats is predated very rapidly and depleted from those areas compared with crab settlement in the shell habitat. Pulses of cohorts could be severely reduced in much less time than the interval between sampling trips and thereafter effectively be unavailable to sculpin in certain areas of the estuary because of virtual removal. Crab that recruit to areas of extensive shell may provide a more stable and persistent prey basis as the dynamics of small instars (agonistic interactions and foraging) make them vulnerable on the exterior of the shell matrix or as they move short distances between shell piles. Predation by sculpin on J1–J4 instars in shell habitats may occur over a longer period, thereby increasing the likelihood that sculpin in our samples contained crab later in the summer, long after they were depleted from less protected areas of open mud and light cover of eelgrass. This would be reflected both in greater numbers of crab consumed and in greater frequency of occurrence

[9] Armstrong, D. A., K. A. McGraw, P. A. Dinnel, R. M. Thom, and O. Iribarni. 1991. Construction dredging impacts on Dungeness crab, *Cancer magister*, in Grays Harbor, Washington, and mitigation losses by development of intertidal shell habitat. Final Rep. FRI-UW-9110 to U.S. Army Corps of Engineers, Seattle District, Seattle, WA, 63 p.

[10] Doty, D., D. A. Armstrong, and B. R. Dumbauld. 1990. Comparison of carbaryl impacts on Dungeness crab (*Cancer magister*) versus benefit of habitats derived from oyster culture in Willapa Bay, Washington. Univ. Washington, Fisheries Res. Inst., Seattle, WA. Rep. FRI-UW-9020, 69 p.



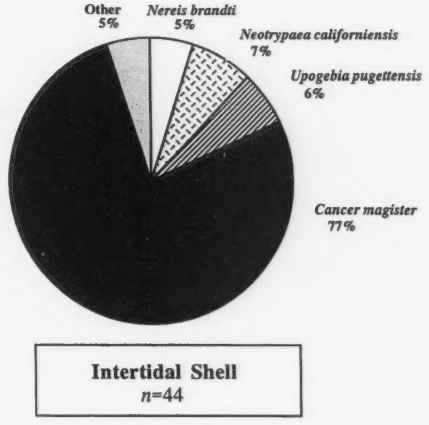


Figure 9

Staghorn sculpin, *Leptocottus armatus*, diets, expressed as % IRI, from intertidal eelgrass and intertidal shell habitats, Grays Harbor, Washington. All data combined, April to August 1989.

in sculpin sampled from the shell habitat (higher %NC and %FO in the IRI calculation).

Size at which 0+ crab were no longer vulnerable to sculpin predation was hypothesized to be about 25 mm CW (about instar J5) (Reilly, 1983) based on mouth gape width of the most prevalent size sculpin (gape limited predation [Zaret, 1980]). Theoretically, small crab newly settled to the estuary would be available and vulnerable to sculpin predation for much of their first full summer (as J1-J6), whereas 1+ crab resident in the estuary during summer would be too large (50–100 mm CW, Fig. 6; Stevens and Armstrong, 1985; Gunderson et al., 1990) for staghorn sculpin to consume. These assumptions were confirmed because only J1–J4 (below 25 mm max. CW) were consumed (Fig. 8). Generally there were relatively few sculpin with an estimated gape width of 25 mm (Fig. 2), thus sculpin were restricted to J1–J4 crab. Carapace width is the larger body dimension of this species of crab, but if attacked from the side (i.e. laterally at the walking legs rather than face-on towards the chelae), then body length (from the posterior of the carapace to the orbit of eyes) could be the limiting dimension with respect to sculpin mouth gape. Based on data of Weymouth and MacKay (1936), the carapace length (CL) of J3, J4, and J5 instars is about 73%, 71%, and 70% of width, respectively. From this perspective, the average size sculpin of this study could possibly consume instars up to J5 with respect to length (approximately 18.8 mm CL). Very few sculpin longer than 175 mm TL were caught; even their estimated gape width was only about 24.6 mm, less than the average carapace width of most 0+ crab by September (Wainwright and Armstrong, 1993).

The six other potential fish predators of 0+ crab found in greatest abundance throughout the summer included juvenile English sole, *Pleuronectes vetulus*, shiner perch, *Cymatogaster aggregata*, snake prickleback, *Lumpenus sagitta*, saddleback gunnels, *Pholis ornata*, sand sole, *Psettichthys melanostictus*, and starry flounder, *Platichthys stellatus*.[2] The first five species have relatively small mouths, are most prevalent as juveniles within the Grays Harbor estuary (English sole) or are not documented as being important crab predators[1] (Williams, 1994). Starry flounder may prey on 0+ Dungeness crab both in Grays Harbor[1] and San Francisco Bay (Reilly, 1983) but are uncommon as adults in the former estuary (Rogers et al., 1989).

The results of this study expand current knowledge of staghorn sculpin's diet composition and feeding behavior, establish the importance of 0+ Dungeness crab as part of the estuarine summer diet of sculpin, and provide a perspective of the potential impact that sculpin predation has on juvenile Dungeness crab survival after settlement. Posey (1986) showed that staghorn sculpin predation limits the distribution of ghost shrimp *N. californiensis* on intertidal sandflats and labeled this fish a keystone predator controlling the depth distribution of newly settled ghost shrimp and the expansion of established beds of adult shrimp. Our data demonstrate that staghorn sculpin are a major predator of small

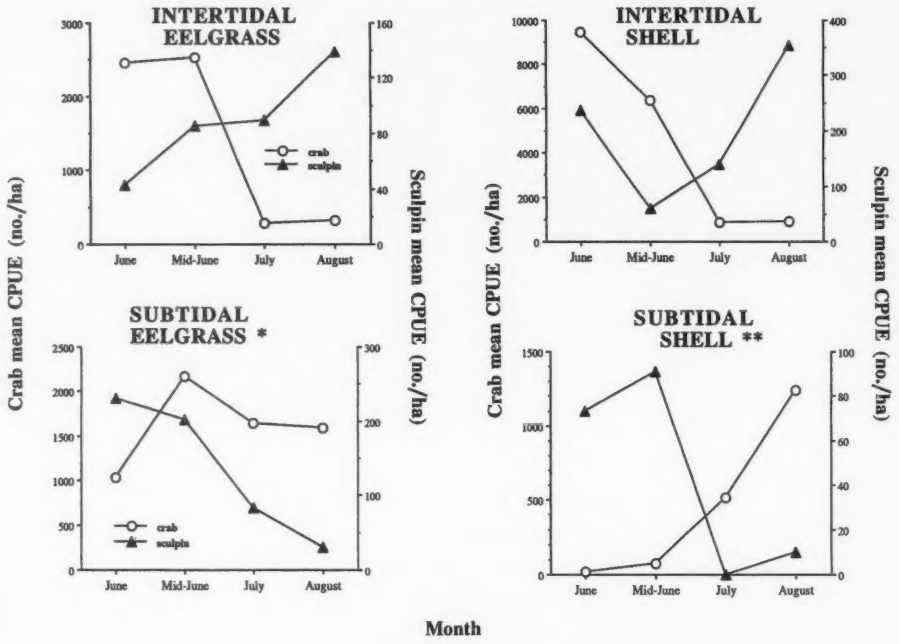


Figure 10

Mean densities of staghorn sculpin, *Leptocottus armatus*, and Dungeness crab, *Cancer magister* (no./ha), from intertidal and subtidal eelgrass and shell habitats, Grays Harbor, Washington, June–August 1989. Note different vertical scales. Each symbol represents the mean CPUE of 2 trawls. * = benthic habitat with shell, ** = benthic habitat with wood and stick material.

0+ Dungeness crab instars during a short period of late spring and early summer settlement and growth and that sculpin may be capable of exerting a pronounced effect on crab year-class strength within coastal estuaries (Armstrong, 1991).

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Larval distribution and transport of penaeoid shrimps during the presence of the Tortugas Gyre in May–June 1991

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Abstract.—As part of the Southeast Florida and Caribbean Recruitment Project (SEFCAR), penaeoid shrimp larvae were collected during the spring and summer cruise of the RV *Longhorn* in the Lower Florida Keys and Dry Tortugas from 29 May to 30 June 1991. Larvae of the pink shrimp, *Penaeus duorarum*, and the rock shrimp, *Sicyonia* sp., were distributed inshore close to the Dry Tortugas Grounds, whereas larvae of the oceanic shrimp *Solenocera* sp. showed mainly an offshore distribution. Significant concentrations of *Solenocera* sp., *Sicyonia* sp., and *P. duorarum* larvae at the Tortugas transect in early June were found within and above the seasonal thermocline while the cold cyclonic Tortugas Gyre was intensively developed. For *Solenocera* sp., which spawn on the outer edge of the gyre, high concentrations of larvae were found at the inshore stations of the Tortugas transect in early June, presumably as a result of the cyclonic circulation of the gyre followed by onshore Ekman transport. *Penaeus duorarum*, which spawn in the shallow Tortugas Grounds, showed a mode of zoea II–III progressing to postlarvae I at the Tortugas Grounds during the 15 days in which the drifter *Halley* recirculated in the interior of the Tortugas Gyre. Retention of *P. duorarum* larvae by the internal circulation of the gyre at the spawning grounds may be an important mechanism for local recruitment of these shrimp to the nursery grounds of Florida Bay.

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Penaeoid shrimps constitute the second most valuable segment of the U.S. fishing industry and are arguably one of the most valuable groups of marine species in the world. Annual stocks fluctuate widely and few spawning stock/recruitment relationships have been demonstrated (Garcia, 1983). The penaeid shrimp *Penaeus duorarum*, or pink shrimp, supports an important commercial fishery in south Florida. Pink shrimp yielded a stable catch of 9.6 million pounds per year from 1960 to 1986 (Klima et al., 1986). However, this catch has declined by more than 50% in the last four years (NMFS[1]). This fishery is directly dependent on young shrimp that migrate from nursery areas onto the fishing grounds (Nance and Patella, 1989). Animals with short life spans (≈2 years), such as pink shrimp, depend almost entirely on one year class being recruited during the year.

The life history of *P. duorarum* of the Dry Tortugas (shallow banks located about 100 km west from Key West) involves one oceanic and one estuarine phase (Garcia and Le Reste, 1981). Adults spawn offshore on the Dry Tortugas, where females lay demersal eggs (Fig. 1). The larvae undergo several changes in feeding habits and morphology including five naupliar stages, three zoeal or protozoeal, and three mysid stages. The last mysis undergoes a moult at which time it transforms into a postlarva. The average time required by *P. duorarum* to reach the first postlarval stage is approximately 20 days at 26°C (Ewald, 1965).

The first postlarval stages are still planktonic whereas those that follow are benthic. Postlarvae migrate inshore, entering the Florida Bay nursery grounds where they metamorphose to juveniles. When they have reached a length of about 10 cm, they return to the Tortugas spawning area (Allen et al., 1980).

Advective processes of *P. duorarum* and their relation to oceanographic and environmental factors are not fully understood. Research on the larval phase was performed in the mid 1960's. Munro et al. (1968) and Jones et al. (1970) studied the abundance and distribution of larvae of *P. duorarum* on the Tortugas Shelf and in the Florida Keys. These authors

[1] Jones, A. Southeast Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, FL 33149. Unpubl. data, 1993.

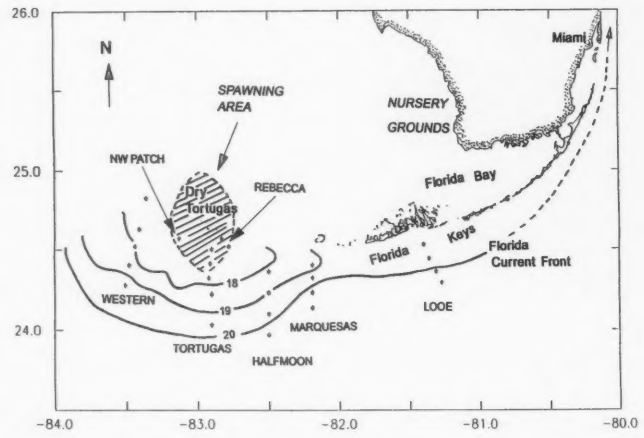

Figure 1

Location of transects and 1-m² MOCNESS sampling stations (*) of the Southeast Florida and Caribbean Recruitment Project (SEFCAR) cruise LH3, 29 May–30 June 1991 at the Dry Tortugas and Lower Florida Keys. Shaded area indicates spawning area of pink shrimp, *Penaeus duorarum*, in southeast Florida. Solid lines are the CTD temperatures at 100 m depth in late May 1991. Dashed line indicates the continuation of the Florida Current.

hypothesized that *P. duorarum* larvae migrate from where they are spawned in the Dry Tortugas by means of the Florida Current and return to Florida Bay through passes in the middle Keys. However, they had difficulty in explaining the exact migratory path in light of inconsistencies between the prevailing currents and the abundance of larvae in the pathway to the coast.

Penaeoid shrimps other than *Penaeus* are abundant in the Dry Tortugas and may occur in commercial catches (Eldred, 1959), but they are of little or no economic value. Such is the case for the rock shrimp, *Sicyonia* spp., the humpback shrimp, *Solenocera* spp., and the roughneck shrimp, *Trachypenaeus* spp. Life histories of these species are poorly known, and larval research in the Gulf of Mexico has focused on trends of seasonal distribution (Eldred et al., 1965; Temple and Fisher, 1967; Subrahmanyam, 1971b).

The Southeast Florida and Caribbean Recruitment Project (SEFCAR) has investigated the effect of oceanographic processes on plankton and regional recruitment of fishes and other reef species along the continental shelf in southeast Florida. The hydrographic conditions in the Straits of Florida are dominated by the strong Florida Current. In the southwestern part of the Florida Keys, the Florida Current is highly variable, often associated with meanders and gyres (Lee et al., 1992). The Dry Tortugas are located near the turning point where the southward-flowing Loop Current swerves abruptly east to enter the Straits of Florida (Gaby and Baig, 1983). A cyclonic gyre over the slope off the Dry Tortugas with horizontal dimensions of approximately 200 km has been described by Lee et al. (1994). The gyre, which persisted for about 100 days from mid-May to late August 1994, was observed to move eastward to the region of the Pourtales Terrace (Lee et al., 1994). Lee et al. (1992) called this gyre the Pourtales Gyre, and its effect on lobster *Scyllarus* sp. and shrimp larvae was demonstrated by the high abundance of larvae nearshore in the path of the westward flow of the gyre (Yeung and McGowan, 1991; Criales and McGowan, 1994).

The objective of this study is to describe the horizontal and vertical distribution patterns of the three most abundant penaeoid shrimp larvae in the Dry Tortugas and lower Florida Keys during the presence of the cyclonic Tortugas Gyre. This work will form a basis for later comparisons with surveys under different hydrographic conditions.

Materials and methods

Plankton and hydrographic sampling

Samples were collected between 29 May and 30 June 1991, as part of the cruise LH3 of the RV *Longhorn*, by using a 1-m² MOCNESS (multiple opening-closing net and environmental sensing system [Wiebe et al., 1976]) with 0.333-mm net mesh size. The nine nets of the MOCNESS were towed in an aperture along an oblique path at a speed of approximately 2 $m \cdot s^{-1}$, and samples from the surface to near the bottom were collected. Net 1 in the set was towed obliquely from the surface down to about 200 m or to the closest multiple of 20 m if the water depth was less than 200 m. Net 2 (deepest) to net 9 (uppermost) sequentially opened or closed at controlled depths of 200–160 m, 160–130 m, 130–100 m, 100–80 m, 80–60 m, 60–40 m, 40–20 m, and 20–0 m for the deeper stations, and 50–40 m, 40–30 m, 30–20 m, 20–10 m, and 10–0 m, or 45–30 m, 30–15 m, and 15–0 m depth intervals for the shallow stations (<50 m). A flowmeter and conductivity-temperature depth (CTD) sensors were attached to the net frame. The volume of water filtered in each layer varied from 130 to 593 m^3, depending on the depth strata sampled.

The cruise was divided into four legs (fifty-six stations) from west of the Dry Tortugas to Looe Key in the middle Florida Keys (Fig. 1). The sampling data are summarized in Table 1. Stations of leg 1 were repeated in the other three legs. During leg 2, one transect was added at Marquesas and another at Halfmoon. Leg 3 repeated stations of legs 1 and 2 in addition to an upstream transect (Western transect). Leg 4 included a downstream transect (Looe Key) in addition to the Tortugas, Rebecca, NW Patch, and Marquesas transects (Fig. 1).

Sampling was carried out continuously depending on the time the ship arrived at the station (Table 1). Samples were taken during the day at 35 stations and at night at the remaining 21 stations. Three moon phases were covered during this cruise. Twenty-six stations were sampled during the full moon, eight during the last quarter, and eight during the new moon.

Three ARGOS satellite-tracked surface drifters were deployed on the northern side of the gyre as part of the physical oceanographic survey. Two stations were sampled on the track of drifter *Halley* after a 15-day interval (day 1=30 May, day 15=13 June).

Larval identification and standardization

Plankton samples were preserved in 4% formaldehyde-seawater solution and later transferred to 70% ethanol. Aliquot sampling was performed after the similarity of duplicate samples was statistically evaluated (t-test, t_9=0.04, P<0.05). Each sample was adjusted to a volume of 500 mL, and the penaeoid larvae sorted from five 25-mL aliquots. The mean of the five counts was standardized to the concentration of larvae (no./100 m^3) or to abundance (no./10 m^2 of sea surface). No nauplii were caught because the mesh size of the net was too large to retain them.

Penaeoid shrimp larvae were identified to genus or species by using existing keys and larval descriptions (Heldt, 1938; Pearson, 1939; Gurney, 1943; Dobkin, 1961; Cook, 1966; Heegaard, 1966; Subrahmanyam, 1971a). Postlarvae of *Penaeus* sp. were identified from the keys of Williams (1965) and the morphometric study of Chuensri (1968). Individual stages were separated only for *P. duorarum* because it was the only species of interest for which larval stages have been described (Dobkin, 1961). The remaining penaeoid identifications were made to a generic level.

Statistical analysis

Mean abundance of total larvae caught at day (0631–2000 h; n=35, $\bar{x}$=98.3, SD=111.6) versus night (2001–0630 h; n=21, $\bar{x}$=91.4, SD=115.5) stations was not significantly different (t-test, t_{54}=0.82, P>0.05); therefore day and night data were pooled (Sokal and Rohlf, 1981).

To characterize the vertical distribution of the different larval stages per species, the depth of the center of mass (Z_m) was calculated (Röpke et al., 1993):

$$Z_m = \sum (P_i \times Z_i)$$

$$P_i = C_i \times H_i \Big/ \sum (C_i \times H_i),$$

where P_i is the standardized (no./100 m^3) number of larvae in the i^{th} depth stratum; Z_i is the mean sampling depth of the i^{th} depth stratum; C_i is the concentration of larvae in 100 m^3; and H_i is the width of i^{th} depth interval. Day and night stations were separated to determine any daily vertical larval migration. Differences in Z_m between day and night were not significant for any of the three species (*P. duorarum* t-test, t_{24}=0.63, P>0.05; *Sicyonia* sp. t-test, t_{36}=0.95; *Solenocera* sp. t-test, t_{50}=0.28, P>0.05), suggesting no daily vertical migration of larvae; therefore data were pooled. However, this may be biased by the greater number of day stations (35 day, 21 night).

Results

Horizontal distribution and abundance

Penaeus duorarum These larvae showed an onshore distribution concentrated near the Dry Tortugas (Fig. 2). The density ranged from 1.5 to 57.1 larvae/10 m^2 represented by 60.3% zoeae, 15% myses, and 24.7% postlarvae. Distribution of zoeae was nearshore; 90% were caught no farther than 25 km offshore from the Dry Tortugas. Myses were distributed a little farther offshore and eastward than zoeae but no more than 45 km from the coast. The trend of distribution of postlarvae was also close to shore; 83% of postlarvae I–III were located inshore at the Tortugas, Halfmoon, NW Patch, and Rebecca transects. The other 17% were found at the offshore stations of Marquesas associated with the Florida Current front, and no postlarvae were captured at the Looe Key transect (Fig. 2).

Larval stages in the spawning area at the NW Patch and Tortugas transects showed a progression of ages during the four legs of sampling (Fig. 3). In late May zoeae II–III showed a high concentration (33.8–45.4 larvae/10 m^2) at the spawning area, few myses were found at these stations, and no postlarvae were caught. In early June, 15 days after the first sampling, the abundance of myses and postlarvae increased. Postlarvae II–III reached their peak of con-

Table 1

Station data and abundance (no./10^2) of penaeoid shrimp larvae during the Southeast Florida and Caribbean Recruitment Project (SEFCAR) cruise LH3, 29 May–30, June 1991.

Station	Latitude N	Longitude W	Max-depth (m)	Distance offshore (km)	Date	Local time (h) (EDT)	Moon phases	Transect	*Penaeus duorarum*	*Sicyonia* sp.	*Solenocera* sp.
Leg 1, 29–31 May											
15	24.498	82.904	25	13.28	29 May	1118 day	Full	Tortugas	12.14	36.43	0.00
17	24.408	82.907	60	25.19	29 May	1242 day	Full	Tortugas	0.00	0.00	56.09
19	24.317	82.916	200	37.03	29 May	1418 day	Full	Tortugas	0.00	0.00	3.46
21	24.222	82.902	207	48.65	29 May	1621 day	Full	Tortugas	0.00	0.00	54.01
23	24.032	82.903	201	73.10	29 May	1754 day	Full	Tortugas	0.00	0.00	0.00
26	24.570	83.125	40	21.50	30 May	1947 day	Full	NW Patch	37.87	29.73	20.60
27	24.559	83.141	40	23.99	31 May	2113 night	Full	NW Patch	41.33	69.10	12.87
Leg 2, 4–7 June											
29	24.500	82.916	20	13.28	4 June	1656 day	Full	Tortugas	19.02	22.83	3.80
30	24.406	82.908	60	25.19	4 June	1816 day	Full	Tortugas	19.76	54.01	129.26
31	24.317	82.916	202	37.03	4 June	2036 night	Full	Tortugas	7.05	52.24	191.50
32	24.227	82.912	203	48.65	4 June	2237 night	Full	Tortugas	0.00	4.04	254.62
36	24.567	83.132	40	22.33	5 June	1946 day	L. quarter	NW Patch	0.00	32.85	100.29
37	24.357	82.500	48	40.28	6 June	1121 day	L. quarter	Halfmoon	36.57	200.21	84.40
38	24.229	82.499	167	47.29	6 June	1243 day	L. quarter	Halfmoon	18.96	35.17	16.64
39	24.103	83.501	197	58.03	6 June	1442 day	L. quarter	Halfmoon	2.86	9.71	21.62
40	23.972	82.503	200	71.39	6 June	1644 day	L. quarter	Halfmoon	0.00	10.46	90.89
42	24.226	82.189	198	30.09	6 June	2334 night	L. quarter	Marquesas	5.28	0.00	16.13
43	24.324	81.194	196	17.47	7 June	0209 night	L. quarter	Marquesas	0.00	0.00	43.38
44	24.403	82.191	77	7.31	7 June	0409 night	L. quarter	Marquesas	0.00	0.00	5.12
Leg 3, 12–18 June											
45	24.568	83.120	40	20.17	12 June	0914 day	New	NW Patch	6.45	3.37	24.84
46	24.833	83.359	56	35.80	12 June	1209 day	New	Western	2.45	0.00	145.05
47	24.634	83.408	57	44.96	12 June	1429 day	New	Western	0.00	0.00	103.36
48	25.524	83.445	125	57.06	12 June	1631 day	New	Western	4.27	6.76	564.17
49	24.401	83.483	202	72.29	12 June	1834 day	New	Western	0.00	0.00	67.77
50	24.280	83.522	200	88.52	13 June	2057 night	New	Western	0.00	0.00	93.78
51	24.032	82.903	200	72.76	13 June	0225 night	New	Tortugas	0.00	0.00	428.11
52	24.222	82.902	203	47.84	13 June	0503 night	New	Tortugas	0.00	0.00	37.43
53	24.317	82.916	202	34.46	13 June	0709 day	New	Tortugas	15.64	7.89	153.24
54	24.408	82.907	58	24.93	13 June	0859 day	New	Tortugas	17.74	26.72	95.20
55	24.498	82.904	21	13.58	13 June	0612 day	New	Tortugas	0.00	5.03	10.74
56	24.524	82.784	17	14.75	13 June	1437 day	New	Rebecca	16.72	22.94	13.72
62	24.403	82.191	57	2.02	17 June	1422 day	New	Marquesas	0.00	4.56	5.94
63	24.324	82.194	162	16.29	17 June	1625 day	New	Marquesas	0.00	2.58	23.66
64	24.226	82.189	162	28.28	17 June	1751 day	New	Marquesas	2.72	10.16	11.50
65	24.133	82.186	159	42.05	17 June	1924 day	New	Marquesas	6.95	17.76	6.00
66	23.972	82.503	160	71.39	17 June	2236 night	New	Halfmoon	0.00	1.95	48.16
67	24.103	82.501	163	58.03	18 June	0107 night	New	Halfmoon	0.00	0.00	50.30
68	24.231	82.501	164	47.29	18 June	0314 night	New	Halfmoon	0.00	0.00	41.40
69	24.360	82.501	15	40.28	18 June	0500 night	New	Halfmoon	0.00	15.09	11.05
70	24.524	82.784	15	14.75	18 June	0638 day	New	Rebecca	20.14	16.60	1.95
71	24.559	83.141	30	19.89	18 June	0938 day	New	NW Patch	17.63	0.00	4.64

centration (18.9 larvae/10 m^2) in mid-June. In late June the peak of zoeae II reoccurred (35.8 larvae/10 m^2).

***Sicyonia* sp.** Rock shrimp was the second most abundant species after *Solenocera* sp. The highest densities were located at the NW Patch and Halfmoon transects (Fig. 4A). Zoeae represented 31.3% of the catch and myses 68.7%. Zoeae were highly abundant at the NW Patch stations in early May (78.8 larvae/10 m^2) and early June (91.1 larvae/10 m^2), and myses were distributed in patches with two large peaks, one at the Halfmoon transect (184.8 lar-

Table 1 (continued)

Station	Latitude N	Longitude W	Max-depth (m)	Distance offshore (km)	Date	Local time (h) (EDT)	Moon phases	Transect	*Penaeus duorarum*	*Sicyonia* sp.	*Solenocera* sp.
Leg 4, 28–30 June											
77	24.032	82.903	160	73.10	28 June	1101 day	Full	Tortugas	0.00	6.60	146.53
78	24.222	82.902	160	48.65	28 June	0140 night	Full	Tortugas	0.00	5.03	10.62
79	24.317	82.916	160	36.46	28 June	1540 day	Full	Tortugas	0.00	4.11	14.38
80	24.408	82.907	57	24.93	28 June	1817 day	Full	Tortugas	1.55	8.60	4.66
81	24.498	82.904	20	13.28	28 June	1827 day	Full	Tortugas	41.34	15.64	0.00
82	24.559	83.141	28	21.95	28 June	2031 night	Full	NW Patch	57.12	151.39	0.00
83	24.570	82.832	15	27.75	28 June	2347 night	Full	Rebecca	14.09	7.05	58.13
85	24.133	82.186	160	36.46	29 June	1616 day	Full	Marquesas	1.72	1.72	3.00
86	24.226	82.189	160	24.93	29 June	1800 day	Full	Marquesas	6.85	2.81	37.73
87	24.324	82.194	158	16.28	29 June	2009 night	Full	Marquesas	0.00	5.75	39.50
88	24.403	82.191	53	2.02	29 June	2148 night	Full	Marquesas	0.00	3.10	23.94
89	24.528	81.395	25	2.16	30 June	0414 night	Full	Looe	0.00	0.00	0.00
90	24.444	81.356	160	11.49	30 June	0443 night	Full	Looe	0.00	0.00	23.69
91	24.361	81.312	161	20.82	30 June	0810 day	Full	Looe	0.00	2.42	33.53
92	24.293	81.269	160	28.27	30 June	2213 night	Full	Looe	0.00	17.31	89.51
									434.20	929.70	3531.90

vae/10 m^2) in early June and the other at the stations of NW Patch transect (60.3 larvae/10 m^2) in late June.

***Solenocera* sp.** This species represented the most abundant penaeoid larvae at the Dry Tortugas and lower Florida Keys, accounting for 72% of the total catch (Fig. 4B). The highest densities were located offshore of the Tortugas and Western transects. Abundances were lowest in late May, increased considerably in early June, and reached their peak in mid-June (Table 1). Of the catch, 29.2% was represented by zoeae and 70.8% by myses. Distribution of early zoeae was patchy; two main peaks occurred at the Western (282.9 larvae/10 m^2) and Tortugas transects (135.4 larvae/10 m^2), and mysid stages were very widely distributed throughout the area with the highest abundance at the Tortugas transect (136.6 larvae/10 m^2) (Fig. 4B). Zoeae and myses showed an offshore distribution, except at stations along the Tortugas transect in early June where high concentrations of *Solenocera* sp. larvae were found at the inshore stations while the Tortugas Gyre was well developed (Figs. 4B and 5).

Vertical distribution

Depths of the center of mass (Z_m) were calculated for the different larval stages of each species (Table 2). *Penaeus duorarum* larvae showed a shallow distribution (Z_m=18 m) which was similar among stages. *Sicyonia* sp. showed a mean Z_m of 27 m, though zoeae were distributed deeper than myses. *Solenocera* sp. larvae were widely spread throughout the water column from 0 to 100 m; the peak concentration occurred at about 42 m, and myses occurred deeper than zoeae (Table 2).

Penaeus duorarum larvae were distributed between temperatures of 23° and 29°C, *Sicyonia* sp. larvae between 20° and 28°C, and *Solenocera* sp. larvae between 15° and 29°C. Maximum concentrations were found between 22° and 26°C (Fig. 5).

Penaeus duorarum postlarvae at the offshore stations of the Marquesas transect (n=6, $Z_m\ \bar{x}$=20.8, SD=14.8) were relatively deeper than those at inshore stations (n=11, $Z_m\ \bar{x}$=11.6, SD=6.7) restricted to the seasonal thermocline (t-test, t_{15}=0.09, P>0.05).

Effect of the Tortugas Gyre on larval abundance and dispersal

Abundance and vertical distribution at Tortugas transect A general downward slope of the upper seasonal thermocline (23–27°C) toward shore was present during the four legs at the Tortugas transect (Fig. 5). *Solenocera* sp., *Sicyonia* sp., and *P. duorarum* larvae were highly concentrated above or within the seasonal thermocline. The strength of the seasonal thermocline, which is uplifted in the interior of the gyre, appears to have been a limiting factor for vertical migrations of these penaeoid larvae.

Solenocera sp. larvae were very abundant at the inshore stations between 25 and 75 m in depth during leg 2, corresponding with the strongly developed

thermocline (Fig. 5). The inshore distribution of *Solenocera* sp. during this leg was noteworthy because these larvae showed an offshore distribution during the other legs.

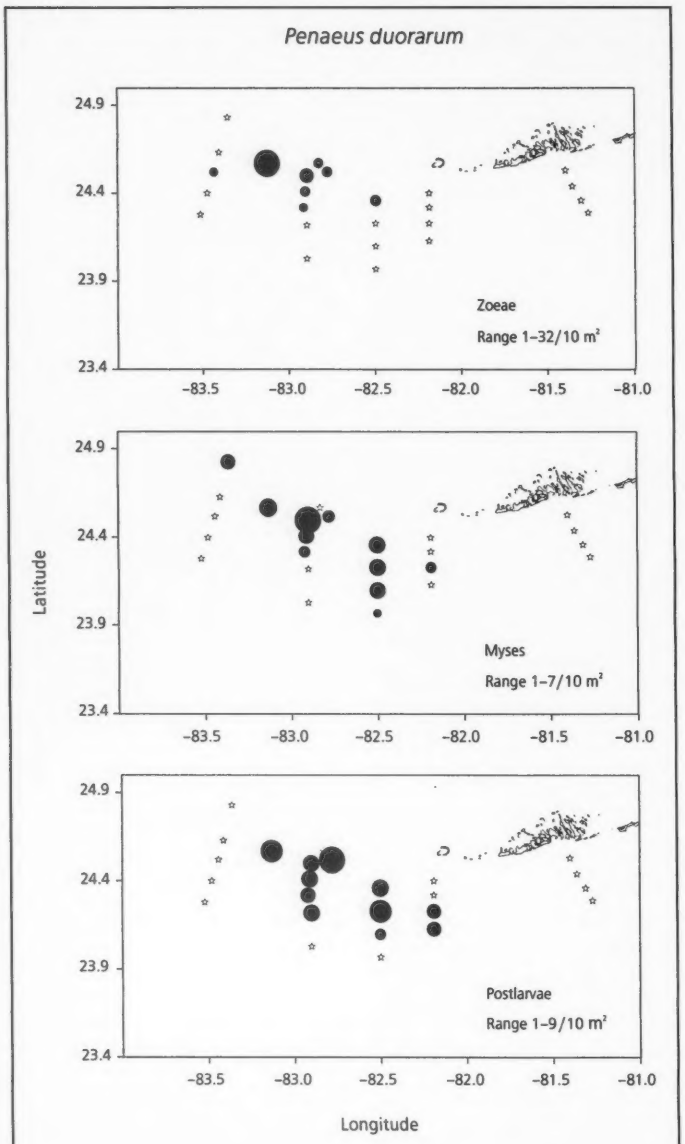

Figure 2

Horizontal distribution and relative abundance (larvae/10 m^2) of the larval stages of pink shrimp, *Penaeus duorarum,* at the sampling stations of the four legs of the LH3 cruise, 29 May–30 June 1991. Symbols are proportional in size to the abundance range and are positioned at the sampling stations. The stars = no catch.

High larval concentrations of the three species (*P. duorarum:* 1–40 larvae/100 m^3; *Sicyonia* sp.: 1–22 larvae/100 m^3; and *Solenocera* sp.: 10–60 larvae/100 m^3) were found at the Tortugas transect during leg 2 in early June within and above the seasonal thermocline between 25 and 75 m in depth (Figs. 5 and 6). Total abundances during leg 2 were much higher than those during any other leg for all three species. The abundance of *Solenocera* sp. was twice as great during leg 2, and there were highly significant differences among legs (ANOVA, $P \leq 0.05$) (Fig. 6).

Drifter circulation Drifter *Halley,* deployed on 30 May on the northern side of the Tortugas Gyre, moved south-southeast for about seven days, then turned back toward the west-northwest for about seven days (Fig. 7). The drifter spent the first 14 days in a tight recirculation in the interior of the gyre. The position of the drifter upon release initially corresponded with the position of stations 26 and 27. On 13 June, when it broke out of the gyral circulation, the drifter was located at Rebecca transect at station 56. At this point the drifter entered the Rebecca Channel between the Dry Tortugas and Rebecca Shoal where it stayed for about 10 days, undergoing tidal excursions of up to 7 km, but with no net through-flow. Relative percentages of the larval stages of *P. duorarum* at the station where the *Halley* drifter was released (Stns. 26 and 27) and at the station where this drifter broke out of the gyre circulation (Stn. 56) are plotted in Figure 7. On 30 May at stations 26 and 27, *P. duorarum* larvae showed one mode of zoeae, mainly II-III (84%). After 15 days, on 13 June, one mode of postlarvae I (67.7%) was present at station 56, a station near the departure point. The trajectory of the drifter *Halley* and the progression of age of *P. duorarum* larvae over the 15 days that the drifter spent recirculating within the gyre may indicate retention of *P. duorarum* larvae at the spawning area.

Abundance and composition of *Sicyonia* sp. larvae at the same two locations, stations 26 and 27, and at station 56 of

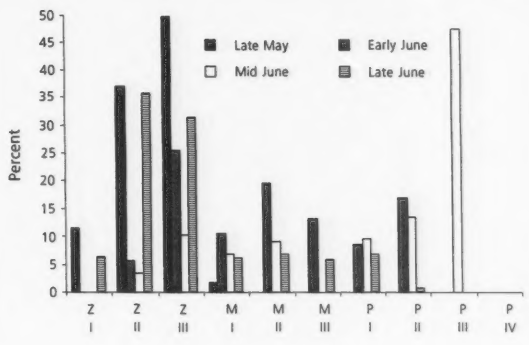

Figure 3

Percentages of the larval stages of pink shrimp, *P. duorarum*, at the Tortugas and NW Patch transects during the four legs of the cruise LH3, 29 May–30 June 1991. Z = zoeae; M = myses; and P = postlarvae.

Rebecca transect showed a similar trend to that described for *P. duorarum*: a high concentration of zoeae at the deployment of the drifter (80% zoeae) and 15 days later a dominance of myses (100% myses).

Discussion

Munro et al. (1968), in an examination of abundance and distribution of *P. duorarum* larvae in southeast Florida, could not reach firm conclusions regarding the path of migration from the Dry Tortugas to Florida Bay because of the inconsistency between the prevailing currents and the abundance of larvae in the pathway to the coast. However, they hypothesized that *P. duorarum* larvae may have been advected from where they were spawned in the Tortugas Grounds by means of the Florida Current and then were carried back into Florida Bay by tidal currents through passes in the middle Keys. The conceptual path of larval advection outlined by Munro et al. (1968) was consistent with the general current pattern known at that time. More recent oceanographic research on the Straits of Florida has shown a high variability in the Florida Current in the lower Keys and Dry Tortugas associated with meanders and gyres (Lee et al., 1992, 1994). Lee et al. (1994) showed from moored current meter data and surface drifter tracks that a cold, cyclonic gyre formed off the Dry Tortugas in mid-May and continued as a weak counterclockwise recirculation about 200 km in diameter until late August. Thus, the presence of the gyre could have acted as a larval retention and recirculation mechanism for the duration of the sampling cruise.

Table 2

Mean and standard deviation of the center of mass ($Z_m \pm$ SD) of the larval stages of three penaeoid shrimps during the SEFCAR cruise LH3, May–June 1991.

	Z (m)	SD	n
Solenocera sp.	42.41	20.97	52
Zoea	35.64	20.08	27
Mysis	42.18	20.69	49
Sicyonia sp.	26.85	17.02	38
Zoea	30.14	20.24	14
Mysis	25.19	13.22	36
P. duorarum	18.42	12.14	26
Zoea	15.00	9.13	15
Mysis	15.07	14.04	15
Postlarvae	16.81	18.67	17

Distributions of zoeae and myses of *P. duorarum* found in this study agree with those of Munro et al. (1968) and Jones et al. (1970) for the Tortugas shelf. However, postlarval distribution in the present study was different; most postlarvae (stages I–III) were located inshore near the area where they were spawned, rather than offshore as was found by Munro et al (1968). Composition of larval stages at the

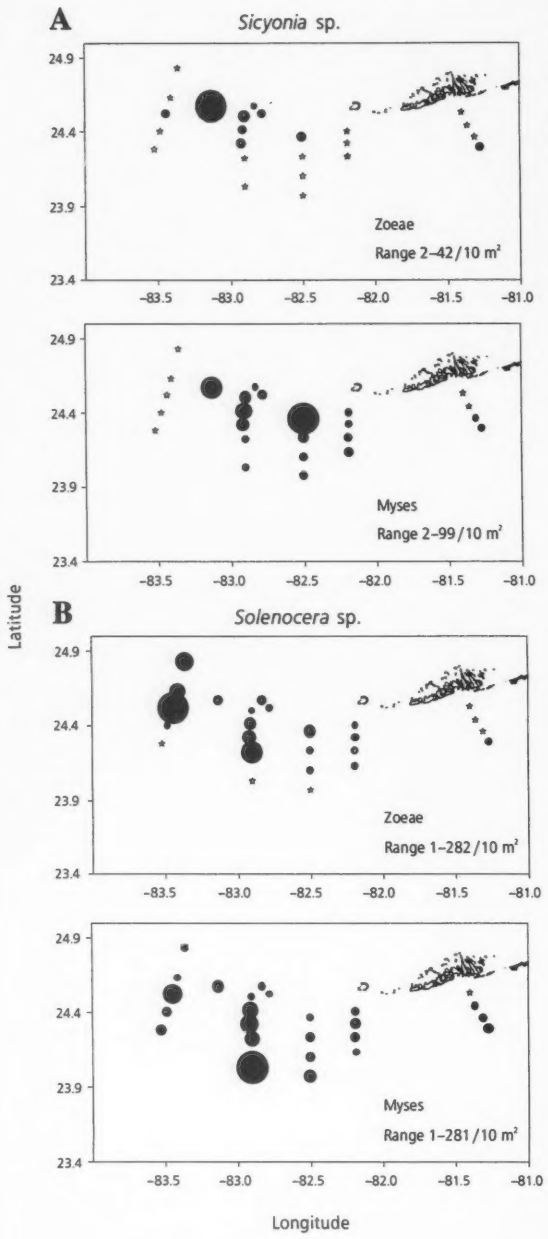

Figure 4

Horizontal distribution and relative abundance (larvae/10 m^2) of zoeal and mysid stages of (**A**) the rock shrimp *Sicyonia* sp. and (**B**) the humpback shrimp *Solenocera* sp. for the four legs of the LH3 cruise, 29 May–30 June 1991. The symbols are proportional in size to the abundance range and are positioned at the sampling stations. The stars = no catch.

Tortugas and NW Patch transects and at the two stations sampled on the track of the drifter *Halley* showed the same modal progression of zoeae to postlarvae within 15 days. This period corresponds to the time reported by Ewald (1965) for zoeae III to become postlarvae I at 26°C. This time period for larval development from zoeae to postlarvae also agrees remarkably well with the trajectory time of the drifter recirculating in the interior of the gyre. The timing of the modal progression of larval stages occurring within those 15 days of gyre recirculation at the spawning area, as shown by the drifter, may indicate that *P. duorarum* larvae were recirculating in the interior of the gyre during development. Interestingly, after the drifter broke out of the gyre circulation it moved toward the east and north toward the Florida Bay shrimp nursery grounds, suggesting a local recruitment pathway for this species.

Retention of *P. duorarum* larvae at the spawning area by the Tortugas Gyre for some days after hatching may enhance the survival of these larvae because food resources are available in the uplifted nutracline where Lee et al. (1994) found maximum concentrations of chlorophyll and copepod nauplii. Furthermore, postlarvae located in the northern (nearshore) portion of the gyre may increase their chance of settling either by escaping the offshore flow on the western side of the gyre entirely or by resisting the offshore flow, thereby drifting to the west rather than being swept offshore (Porch, 1993). Thus, the primary pathway for *P. duorarum* larvae to reach the nursery areas of Florida Bay may include retention at the spawning area by recirculation in the Tortugas Gyre followed by movement onto the Southwest Florida shelf and Florida Bay by wind and tidal currents. Those larvae that are advected eastward by the Florida Current may reach the upper and middle Keys. The latter alternative could explain the great number of postlarvae found in the middle Keys by Munro et al. (1968) and Roessler and Rehrer (1971).

Sicyonia sp. larvae showed a coastal and shallow distribution. Young zoeae were generally restricted to the inshore stations, indicating that this species may spawn near the Dry Tortugas Grounds. Myses showed the highest concentrations inshore, with a maximum concentration at the Marquesas transect. Larval stages at the two stations of the drifter showed a similar trend to that of *P. duorarum*. The time of development of *S. brevirostris* from spawn-

ing to the first postlarval stage is approximately 30 days (Cook and Murphy, 1965). Local retention of larvae at the spawning area followed by recruitment into the coastal region may be the migration mechanism for this coastal and short-lived species as well.

Early-stage zoeae of *Solenocera* sp. were widely distributed offshore; two main peaks were located at the Western and Tortugas transects at a depth of about 35 m. The age of these zoeae was estimated to be 3 to 5 days in accordance with Heldt's description (1938) of the larval development of *S. membranacea*. These data indicate that this species may have spawned somewhere in the Gulf of Mexico in a location corresponding to the outer edge of the Tortugas Gyre. Myses showed an offshore distribution in all but the Tortugas transect during leg 2, where most larvae were found inshore. The great concentration of *Solenocera* larvae at the inshore stations of the Tortugas transect in early June between 25 and 75 m in depth corresponded with the strongly developed

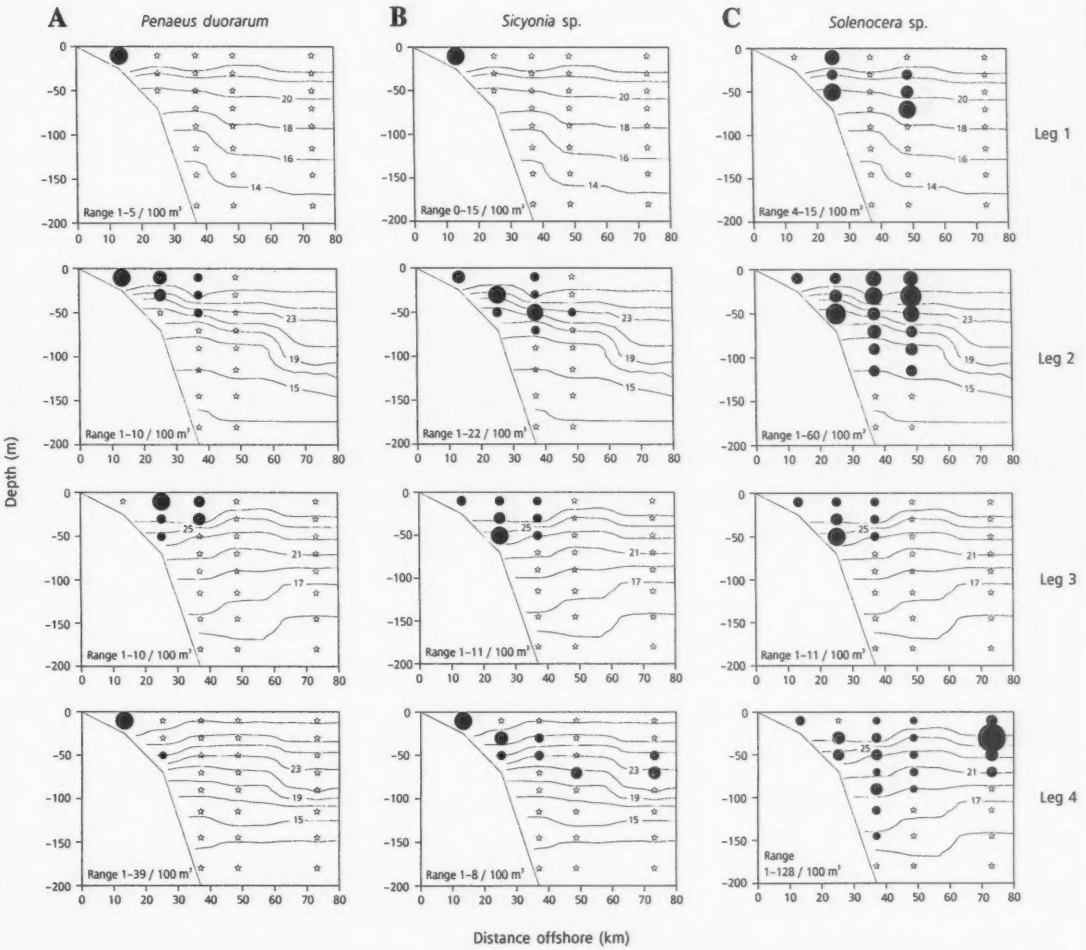

Figure 5

Cross section of Tortugas transect during the four legs showing the vertical distribution and relative concentrations (larvae/100 m^3) of the three penaeoid species: pink shrimp, *Penaeus duorarum* (**A**); the rock shrimp *Sicyonia* sp. (**B**); and the humpback shrimp *Solenocera* sp. (**C**), superimposed over the vertical temperature profiles (°C) from the MOCNESS temperatures. Symbols are proportional in size to the abundance range. The stars = no catch.

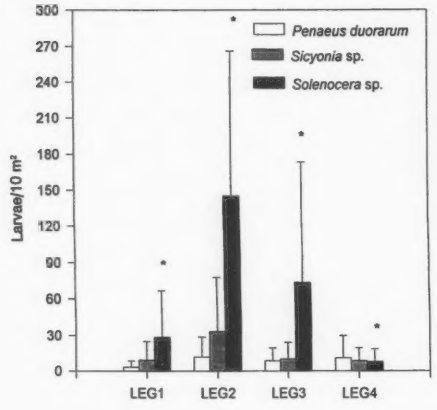

Figure 6

Mean relative abundance (larvae/10 m^2) and standard deviation of the pink shrimp, *Penaeus duorarum*, the rock shrimp *Sicyonia* sp., and the humpback shrimp, *Solenocera sp.*, at the sampling stations of the Tortugas transect during the four legs of the LH3 cruise, 29 May–30 June 1991. (*) = significant differences in mean relative abundance between legs, within species ($P \leq 0.05$).

thermocline as a consequence of the Tortugas Gyre. Criales and McGowan (1994) found *Solenocera* larvae in high abundance (62% of the penaeoid larvae) at an inshore station of Looe Reef transect during the presence of the Pourtales Gyre, whereas few larvae (only 15%) were captured in the absence of the gyre when the Florida Current intruded close to the coast.

The combination of the cyclonic gyre circulation and inshore surface Ekman transport convergence should result in a concentration of larvae in the interior of the gyre and in an onshore transport in the eastern portion. Onshore Ekman transport is expected to be relatively high in the Lower Keys and Dry Tortugas where prevalent southeast winds favor onshore transport toward the east-west oriented coast. The importance of Ekman transport on recruitment has been shown in the Florida Keys for *Scyllarus* larvae (Yeung and McGowan, 1991) and for other decapod larvae particularly brachyuran larvae in other regions (see Hobbs et al., 1992; McConnaughey et al., 1994).

Substantial gaps exist in our knowledge of the life histories of penaeoid shrimps. For example, larval development of *Solenocera* spp. has not been conducted for any of the five western Atlantic species (Perez-Farfante and Bullis, 1973), and larval development of only one of the seven western Atlantic species of *Sicyonia* spp. is known (Cook and Murphy, 1965). As long as our knowledge of the life history and larval development of these species remains limited, further conclusions regarding interactions of recruitment processes with the physical environment will remain uncertain.

This research showed the effects of the Tortugas Gyre circulation on dispersal and abundance of local coastal (*P. duorarum* and *Sicyonia* sp.) and oceanic (*Solenocera* sp.) shrimp species. The modal progression of *P. duorarum* zoeae to postlarvae within the same 15-day period in which the gyre recirculated in the Tortugas region indicates that *P. duorarum* larvae, in addition to the advective process postulated by Munro et al. (1968), may recirculate within the gyre during their development. Retention of larvae by the gyre circulation at the Dry Tortugas, combined with wind driven transport on the southeast Florida shelf, is a plausible recruitment pathway for pink shrimp recruiting to the nursery grounds of Florida Bay.

Acknowledgments

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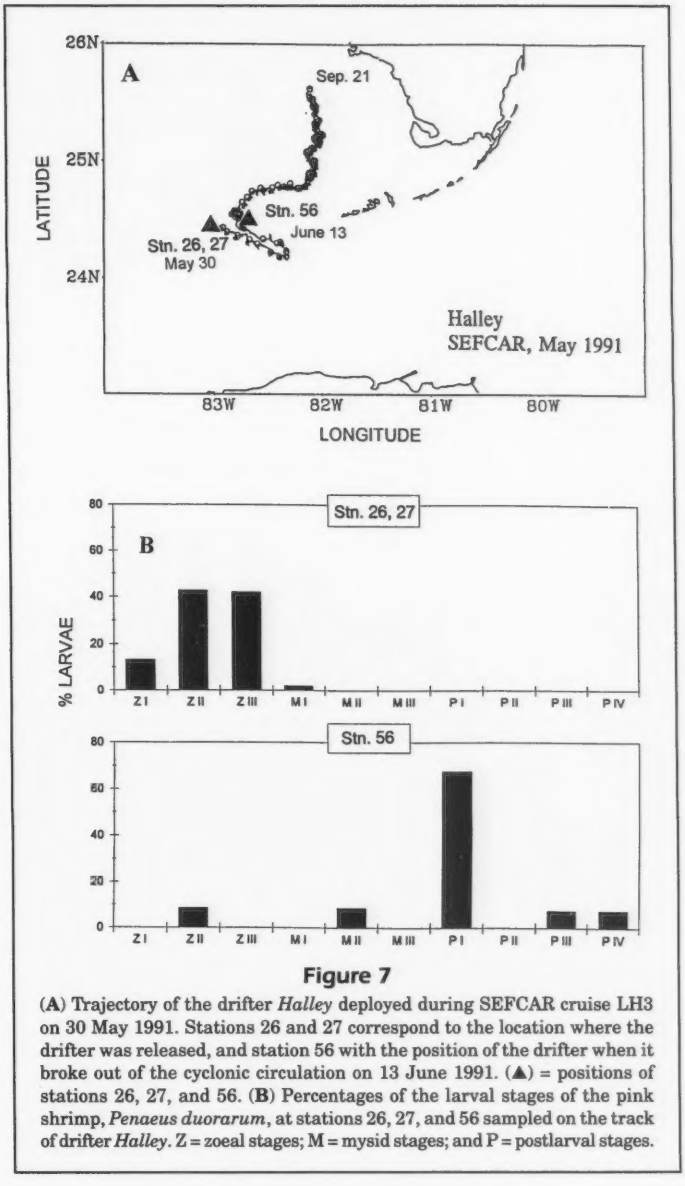

Figure 7

(A) Trajectory of the drifter *Halley* deployed during SEFCAR cruise LH3 on 30 May 1991. Stations 26 and 27 correspond to the location where the drifter was released, and station 56 with the position of the drifter when it broke out of the cyclonic circulation on 13 June 1991. (▲) = positions of stations 26, 27, and 56. **(B)** Percentages of the larval stages of the pink shrimp, *Penaeus duorarum*, at stations 26, 27, and 56 sampled on the track of drifter *Halley*. Z = zoeal stages; M = mysid stages; and P = postlarval stages.

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Growth and reproduction of the common dolphin, *Delphinus delphis* Linnaeus, in the offshore waters of the North Pacific Ocean

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Abstract.—A total of 707 common dolphins, *Delphinus delphis* Linnaeus, (376 males and 331 females) taken in Japanese, Korean, and Taiwanese drift nets in the central North Pacific Ocean from February to November 1990 and 1991 were examined. Sex, total length, date, and location of capture were recorded. Biological samples were collected from 152 of the dolphins examined (93 males and 59 females). Ages were determined by counting dentinal layers. Female reproductive status was determined by macroscopic examination of ovaries (n=43). Eight females were mature, two were pregnant, three were resting, two were lactating, and one was of unknown condition. Testes and epididymes were examined for evidence of spermatogenesis (n=70); 21 males were mature. A preliminary estimate of gestation period was 11.1 months. The sex ratio appeared to favor males; segregation during the sampling period may be responsible for differences from 1.0. Male average age at sexual maturation was estimated to be 10.5 years. The largest sexually immature male was 179 cm; the smallest sexually mature was 182 cm. Mature testis weights ranged from 273.2 g to 1,190 g. Females reached sexual maturation at about 8.0 years; estimates of length at sexual maturation were 172.8 and 170.7 cm. Predicted asymptotic lengths for males and females were 188.1 cm and 179.4 cm, respectively. Calving appeared to peak in May and June. Sampling effort moved northward through September; infrequent sampling of parturient females and neonates during the projected calving mode suggests they were segregated outside the fishing area at that time.

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The common dolphin, *Delphinus delphis* Linnaeus, is an oceanic species widely distributed throughout the tropical and temperate seas of the world. In the western North Pacific Ocean, published accounts have dealt almost exclusively with taxonomy, distribution, and seasonal movements (Ogawa, 1937; Nishiwaki, 1967; Kasuya, 1971; Ohsumi, 1972). The common dolphin has been studied most extensively in the eastern North Pacific Ocean where research has focused primarily on species distribution, herd movements, reproductive seasonality, stock differences, and behavior (Norris and Prescott, 1961; Brownell, 1964; Hui, 1979; Evans, 1982; Perrin et al., 1985; Perryman and Lynn, 1993; Heyning and Perrin, 1994; Walker and Cowan[1]; Walker et al.[2]).

Two morphotypes of common dolphin, a short-beaked form and a long-beaked form, differing in rostral length, overall size, and color pattern, have been described from southern California waters (Banks and Brownell, 1969; Evans, 1975). Heyning and Perrin (1994) described two species of *Delphinus* from the eastern North Pacific Ocean, a short-beaked form which is referable to *D. delphis* Linnaeus and a long-beaked form assigned to the nominal species *D. bardaii* Dall, 1893. Recent studies of molecular genetics confirm the morphologic findings and support distinction of these two morphotypes of common dolphin as separate species (Rosel et al., 1994).

Despite the abundance of *D. delphis* in the eastern North Pacific Ocean, little biological information on age, growth, and reproductive condition exists in the literature. Ridgway and Green (1967) and Harrison et al. (1972) present gonadal data for a total of 30 male and 25 female specimens collected over a 16-year period from single strandings or live-capture. Correlations with age were not incorporated in either study. Hui (1979) correlated age, reproductive condition, and flipper bone development and summarized

[1] Walker, W. A., and D. F. Cowan. 1981. Air sinus parasitism and pathology in free-ranging common dolphins, *Delphinus delphis*, in the eastern tropical Pacific. Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038. Admin. Rep. LJ-81-23C, 19 p.

[2] Walker, W. A., F. G. Hochberg, and E. S. Hacker. 1984. The potential use of parasites *Crassicauda* (Nematoda) and *Nasitrema* (Platyhelminthes) as biological tags and their role in the natural mortality of common dolphins, *Delphinus delphis*, in the eastern North Pacific. Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038. Admin Rep. LJ-84-08C, 31 p.

data on age and gonadal condition for 35 male and 52 female specimens. Most of the dolphins examined in this study were collected during purse-seine research operations off the southern California coast (Hui, 1973).

In the late 1970's, Japan, Taiwan, and the Republic of Korea initiated high-seas driftnet fisheries for flying squid, *Ommastrephes bartrami*, and large-mesh fisheries for pelagic fish species including albacore tuna, *Thunnus alalunga*. The majority of squid driftnet fisheries operated from June to November in the central North Pacific Ocean between lat. 34°–46°N and long. 171°E–147°W, while large-mesh fisheries operated farther south and west between lat. 29°N–45°N and long. 147°E–150°W from February to November. *Delphinus delphis* was the most frequently killed cetacean in the large-mesh fisheries and was also found regularly entangled in the squid driftnet fisheries (Hobbs and Jones, 1993).

Beginning in 1990, under international cooperative agreements, biological samples were collected from marine mammals killed in the Japanese and Taiwanese squid and large-mesh fisheries and from marine mammals killed in the Korean squid fishery. Combining the 1990 and 1991 biological samples provided an opportunity to estimate growth and reproductive parameters for *D. delphis* from the offshore waters of the North Pacific Ocean.

Materials and methods

Specimen collection

Scientific observers collected biological data from all cetaceans caught in Japanese, Korean, and Taiwanese driftnet operations. Soon after arrival on deck, each cetacean was identified, sexed, measured (total length to nearest 1.0 cm), photographed twice (left lateral and ventral), and given an individual specimen number.

When an animal was dissected, the left lower jaw was tagged and frozen intact. For males, the right testis and epididymis were collected whole, tagged, and preserved in 10% formalin. Females were checked for evidence of lactation by longitudinal incision through the left mammary gland. The ovaries and uteri for most females were collected intact. The left ovary and entire reproductive tract was tagged and preserved in 10% formalin. If the animal was pregnant with a large fetus or was recently postpartum, only the ovaries and a cross section of the left uterine horn were collected. Fetuses were sexed, weighed to the nearest 1.0 g, and measured to the nearest 1.0 cm.

Frozen and preserved samples were shipped to the National Marine Mammal Laboratory in Seattle, Washington, for analyses.

Age determination

Teeth were extracted from the center of the left lower jaw for age determination. Each tooth was decalcified and sectioned (24 μm) longitudinally on a freezing microtome. Tooth-section preparation and dentinal growth-layer group (GLG) counting procedure followed guidelines developed by Myrick et al. (1983) for *Stenella* spp. Six to eight stained sections from the center of each tooth were mounted on a glass slide and examined under a compound microscope at 40× and 100× magnification with transmitted light. Dentinal GLG characteristics have been described for *Delphinus* (Perrin and Myrick, 1981). Annual deposition of dentinal GLG's has been established for tetracycline-marked common dolphins (Gurevitch et al., 1981). We followed these findings and assumed one GLG represented one year of growth.

Each tooth was read independently by two readers. Ages were recorded to the nearest 0.5 layer except for animals with less than one complete GLG. In these cases, we estimated the thickness of the incomplete layer to the nearest 0.2 GLG. Predetermined limits on reader variability were established following those used for *Lissodelphis borealis* in Ferrero and Walker (1993). This procedure allowed for a 0.5-layer difference between readings for estimated ages up to 5 years (measured from the median reading), one layer for estimates between 5 and 10 years, and one additional layer for every 5-year interval thereafter. Within these limits, we averaged the two readers' estimates to obtain the final age. When readings differed by more than these limits, the tooth was reread.

Examination of reproductive organs

Males Right testes with epididymides were weighed to the nearest 0.01 g and measured to the nearest 0.1 cm. A 1-cm^3 block was removed from the center of each testis; a similar section of epididymis was removed at mid-length, and both were prepared for histological analysis. Paraffin-embedded tissues were sectioned at 6 μm, stained with hematoxylin and eosin, and mounted on glass slides. Testes and epididymides were examined for evidence of spermatogenesis by using a compound microscope at 100× with transmitted light. Males were considered mature if sperm were present in testes tubules.

Females Ovaries were weighed to the nearest 0.01 g. Maximum diameter of the left uterine horn was

measured to the nearest millimeter. Each ovary was sliced transversely into serial sections (≈1 mm thick) with a scalpel and examined for the presence of corpora lutea and corpora albicantia. Two measurements of corpus diameter, taken at right angles, were recorded for well-regressed corpora; three diameters were recorded for larger corpora. Total corpus counts included corpora albicantia and corpora lutea from both the right and left ovaries. Females were classified as sexually mature if at least one corpus was present on either ovary.

Corpora were examined externally for indications of regression, including color change (i.e., darkening), reduced size and surface furrowing, and were classified by type following Perrin et al. (1976).

Results

The sample

From February to December 1990 and 1991, a total of 707 *D. delphis* (376 males and 331 females) were examined (see Fig. 1 for approximate collection locations). Sex, length, collection date, and location were recorded for each specimen, and biological samples were collected from 152 of these dolphins (93 males and 59 females).

Postnatal growth patterns and the reproductive parameters, average age and average length at sexual maturation, were measured by using the portion of the dissected sample for which both age and reproductive status were determined (70 males and 43 females). We tested for differences in the length distributions of the total sample and the reproductive sample; no significant differences were detected (Kolmogorov-Smirnov Test, D=0.18, P>0.05) The total sample (n=707) was used to examine sex ratios, gestation period, and reproductive seasonality. The spatial and temporal distribution of the total sample reflects the movement of the driftnet fisheries northward from February to August, then southward in the fall (Gong et al., 1993; Nakano et al., 1993; Yatsu et al., 1993; Yeh and Tung, 1993; Table 1).

Male *D. delphis* ranged from 0.4 to 27 years in age (n=93): 3% were calves <1 year old (n=3), 23% were yearlings (n=21), and the remainder were >2 years old. Female ages ranged from 0 to 26 years (n=59); one newborn was sampled, 5% were calves <1 year old (n=3), and 32% were yearlings (n=19). The age distribution of both sexes (Fig. 2) declined intrinsically except between the two youngest age groupings.

Males ranged in length from 86 to 211 cm. Females ranged from 81 to 199 cm (Figs. 3 and 4).

Stock identification

The two recently described species of common dolphin in the North Pacific Ocean are separable on the basis of cranial morphometrics and color pattern (Heyning and Perrin, 1994). To date five cranial specimens are available from the driftnet fisheries and of these, one is from an adult animal. The rostral length to zygomatic width ratio for the single adult specimen (201 cm, male) was 1.36. The mean ratio for adult male short-beaked common dolphin presented in Heyning and Perrin (1994) was 1.37 (SE=0.046). Preliminary comparison of photographs of common dolphins taken in the driftnet fisheries (color pattern features are described in Heyning and Perrin [1994]) suggests that our sample more closely resembles the short-beaked common dolphin. Furthermore, the currently known distribution of both species of *Delphinus* presented in Heyning and Perrin (1994) indicates that only the short-beaked form of

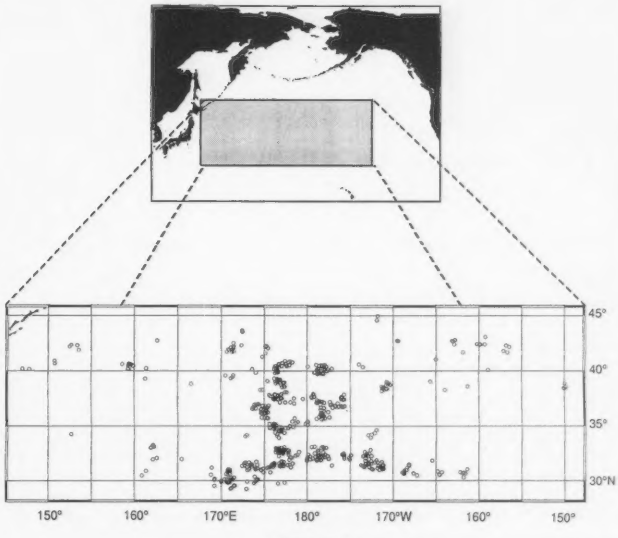

Figure 1

Approximate sampling locations of 376 male and 331 female common dolphin, *Delphinus delphis*, caught in Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991.

Table 1

Number of *Delphinus delphis* specimens examined from February to December, 1990 and 1991, from latitudes 29°N to 44°N in Japanese, Korean, and Taiwanese drift nets.

	Latitude (in degrees)															
Month	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
February	1	9	8	0	0	0	0	0	0	0	0	0	0	0	0	0
March	15	41	92	15	0	0	0	0	0	0	0	0	0	0	0	0
April	0	4	10	103	10	0	0	0	0	0	0	0	0	0	0	0
May	0	0	0	0	0	53	24	0	0	4	0	0	0	0	0	0
June	0	0	0	0	0	0	15	46	59	33	6	8	0	0	0	0
July	0	0	0	0	0	0	0	0	0	2	21	37	2	13	0	0
August	0	0	0	0	0	0	0	0	0	0	1	11	0	5	2	2
September	0	0	0	0	0	0	0	0	0	0	0	0	2	6	0	0
October	0	0	0	0	0	0	0	0	0	0	0	21	12	4	0	0
November	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
December	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

common dolphin extends into the driftnet fisheries area of the central North Pacific Ocean. On the basis of these factors, we provisionally assign the *Delphinus* in our sample to the short-beaked common dolphin *D. delphis*.

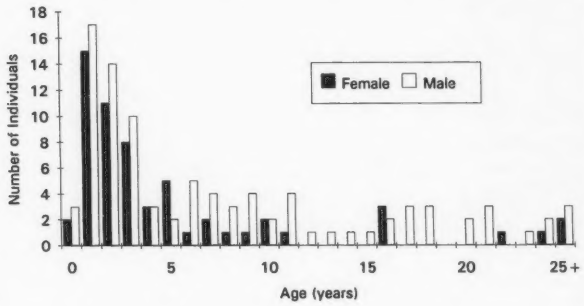

Figure 2

Age-frequency distribution of 93 male and 59 female common dolphin, *Delphinus delphis*, caught in Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Growth

Length at birth and gestation period

Only two fetuses (65.0 cm and 12.6 cm) and one age-0 neonate (82 cm) were collected; this small sample size limited our ability to calculate a length at birth with the method described by Hohn and Hammond (1985) or the modified DeMaster (1978) approach described by Ferrero and Walker (1993).

The small sample size of newborns and lack of near-term fetuses also limited estimation of the gestation period. However, if we assume that the length of the age-0 neonate approximates the size at birth (82.0 cm) and consider the collection dates and lengths of the two fetuses, then preliminary estimates can be determined. We explored the gestation period parameter in two ways: 1) by using the relationship between fetal length and time described by Hugget and Widdas (1951), and 2) by using the relationship between size at birth and gestation period described for several species of delphinids by Perrin et al. (1977).

Following Hugget and Widdas (1951), we regressed the lengths (y) of our two fetus specimens and the age-0 neonate (we assumed this animal was recently born given the complete absence of postnatal dentine) on time, indexed by day of the year of collection (x), in order to estimate the linear phase of growth (t_g–t_o), where t_g is the gestation period and t_o is the "nonlinear" phase of growth. The regression equation

$$y = -57.04 + 0.264x \quad (1)$$

was significant (r^2=0.996, P<0.001). The linear growth phase was estimated to be 10.5 months. We did not attempt to estimate the nonlinear phase be-

cause an empirical method for doing so is lacking (Perrin and Reilly, 1984).

We also used Perrin et al.'s (1977) regression equation:

$$\text{Log}(y) = 0.1659 + 0.4586\,\text{Log}(x), \quad (2)$$

substituting x with the length of our age-0 neonate. The *D. delphis* length at birth estimate of 82.0 cm approximated the gestation period at 11.1 months.

Postnatal growth Growth curves were fitted separately for males and females by using a nonlinear least-squares method. The Laird/Gompertz formula (Laird, 1969) was used as a base model for both sexes:

$$L(t) = L_0 \exp\{a[1-\exp(-\alpha t)]\}, \quad (3)$$

where $L(t)$ is the length at age t, L_0 is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth.

For both sexes, we fit two Laird/Gompertz curves, one for the sexually mature animals and the other for the sexually immature, in order to minimize the number of positive residuals in the upper curve segment. The low sample size prohibited attempts to iteratively fit the two curve segments and locate the intersection point.

Female growth through age 2 was rapid, with a predicted length at age of 146.4 cm. The predicted asymptotic length was 179.4 cm (Fig. 5).

The male growth curve through age 2 was slightly steeper than that portion of the female growth curve, reaching a predicted length at age of 149.8 cm. The predicted asymptotic length was 188.1 cm (Fig. 6).

The mean length of females age 16 and older (i.e. those animals likely to have reached maximum size based on the predicted length at age [16 yr] falling on the asymptotic portion of the upper growth curve) was 179.8 cm (n=5, SE=6.76). The mean length of males age 16 and older was 187.1 cm (n=15, SE=5.57). The difference in mean lengths between sexes was significant (t-test, one-tailed, P=0.04).

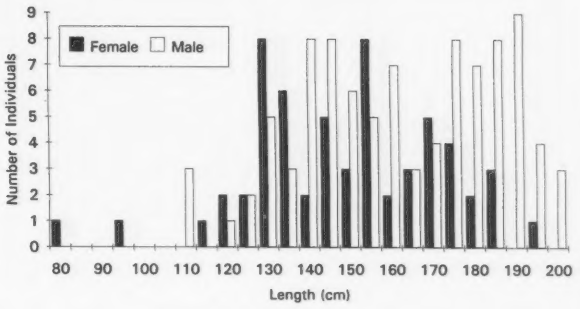

Figure 3

Length-frequency distribution of 93 male and 59 female common dolphin, *Delphinus delphis*, for which ages were determined. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

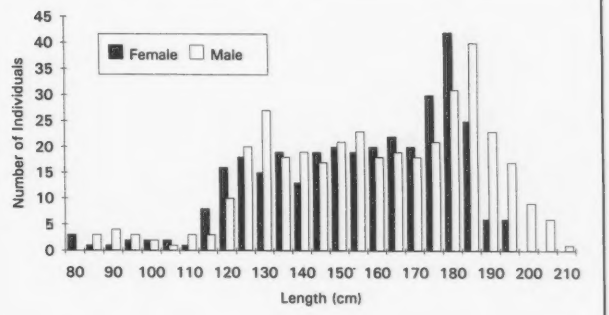

Figure 4

Length-frequency distribution of all common dolphins, *Delphinus delphis*, examined at sea February–November 1990–91 (376 males and 331 females). Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Reproduction

Sex ratio Sex ratios were estimated for four subsets of the aggregate sample of measured animals (n=707) to represent progressively older age groups. The predicted length at age from our postnatal growth models (Figs. 5 and 6) were used to separate the sample into four approximate age groups (≤1 year, 1 to 10 years, 10 to 15 years, and >15 years) on the basis of length. In addition, we calculated separate sex ratios for the portions of the sample collected north and south of 34°N latitude. The latitudinal break corresponded to a break in the timing of collections, splitting February, March, and April sampling from the remainder of the year (Table 1). We used the empirical logistic transform method (Cox and Snell, 1989) to estimate sex ratio as

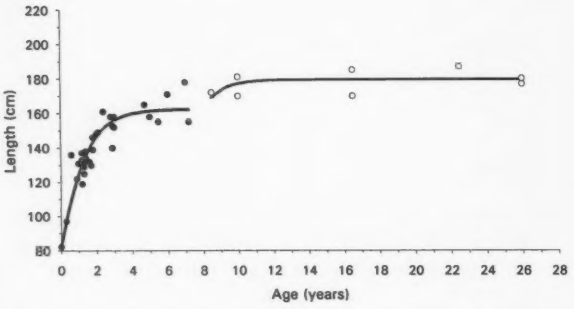

Figure 5

Age at length of female common dolphin, *Delphinus delphis*, with fitted growth curves (Laird/Gompertz model). The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

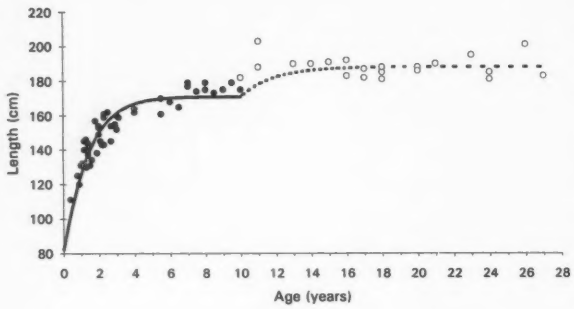

Figure 6

Age at length of male common dolphin, *Delphinus delphis*, with fitted growth curves (Laird/Gompertz model). The open circles are mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

$$r = \frac{m+0.5}{f+0.5}, \tag{4}$$

where r is the ratio of males to females, m is the number of males, and f is the number of females. The natural logarithm of r is normally distributed with variance,

$$\mathrm{var}[\ln(r)] = \frac{(n+1)(n+2)}{n(m+1)(f+1)}, \tag{5}$$

where n is the total number of males and females, m is the number of males, and f is the number of females. Of the sex ratios calculated by using the sample collected from all areas, only the 10 to 15 year-old group ratio (1.792) was significantly different from 1.0 (Exact Binomial Test, $P<0.01$). When only the portion of the sample collected south of 34°N was considered, none of the ratios was significantly different from 1.0 (P-values were all >0.2). The sample collected north of 34°N yielded a sex ratio significantly different from 1.0 (Exact Binomial Test, $P<0.01$) in the 10 to 15 year-old group (2.641) (Table 2).

Average age at sexual maturation Only preliminary estimates of average age at sexual maturation (ASM) could be calculated owing to the insufficient number of indeterminant age classes represented in the sample. No indeterminant age classes were represented in the female sample. For males we used the DeMaster (1978) method which computes the mean age as

$$ASM = \sum_{a=j}^{k} a(f_a - f_{a-1}), \tag{6}$$

where f_a is the fraction of mature animals in the sample aged a, j is the age of the youngest mature animal in the sample, and k is the age of the oldest immature animal in the sample.

Maturity status overlapped one age class in the male sample, where we estimated the variance as

$$\mathrm{var}(ASM) = \sum_{a=j}^{k} \frac{f_a(1-f_a)}{(N_a - 1)}, \tag{7}$$

where N_a is the total number of animals aged a.

Males The preliminary estimate of average age at onset of sexual maturation for males was 10.5 years (SE=0.50). Only at age 10 did both sexually mature and immature specimens appear in the sample.

There was a significant linear correlation between testis weight and age among the immature animals (r^2=0.83, $P<0.01$), but the overall increase in testis weight was small (<50 g over 10 years). A linear relationship between age and testis weight was not apparent among mature animals (r^2=0.15). Testis weight dramatically increased after age 10 (Fig. 7A).

The sample contained 21 sexually mature and 50 sexually immature males. The testis weight of the

youngest sexually mature male (10 years) was 370 g; the testis weight of the oldest immature (10 years) was 34.6 g. Weights of mature testes ranged from 273.2 to 1,190 g.

Females Only a rough approximation of female average age at sexual maturation was determined. The oldest sexually immature female was age 7.2 years, and the youngest sexually mature was 8.5 years. Of the forty-three female reproductive tracts collected, 8 were from mature animals. The youngest sexually mature female had three corpora (Fig. 8A). Of the mature females, three were resting, two were pregnant, two were lactating and had stage-2 corpora, and one was of unknown status (Table 3).

Average length at sexual maturation Calculation of average length at sexual maturation was limited for the male sample because no indeterminant length classes were represented. The female sample was adequate to estimate the parameter. Two methods were used: the DeMaster (1978) method, modified to estimate the average length instead of average age, and a logistic regression method.

The modification of DeMaster's method, applied to females, used lengths grouped into even intervals as

$$LSM = \sum_{i=i_{\min}}^{i_{\max}} l_i (f_i - f_{i-1}), \qquad (8)$$

where i_{min} is the index of the size class with the smallest mature animal, i_{max} is the index of the size class with the largest immature animal, l_i is the lower limit of the ith size class, and f_i is the fraction mature in the ith size class.

The variance estimate on female LSM was obtained by modifying the formula of DeMaster (1978) to account for the interval width (w) so that

Table 2

Sex ratios for four age groups of *Delphinus delphis*. Predicted lengths at age from the Laird/Gompertz growth model were used to determine the upper limits for each group (i.e. 125 cm, both sexes ≤1 year; 171 cm for males and 169 cm for females aged 1 to 10 years; 187 cm for males and 179 cm for females aged 10–15 years). Sex ratios significantly different from 1.0 (α=0.05) are marked with an asterisk. SE = Standard error.

Area and age groups	No. of individuals		Sex ratio	SE
	Male	Female		
All areas				
≤ 1	32	41	0.7831	0.2342
1–10	182	161	1.1362	0.1079
10–15	90	50	1.7921*	0.1756
>15	71	79	0.8994	0.1630
South of 34°N latitude				
≤ 1	11	18	0.6216	0.3750
1–10	78	72	1.0828	0.1629
10–15	39	31	1.2540	0.2388
>15	24	35	0.6901	0.2625
North of 34°N latitude				
≤ 1	21	23	0.9149	0.2985
1–10	105	89	1.1788	0.1437
10–15	51	19	2.6410*	0.2649
>15	47	44	1.0674	0.2086

$$\mathrm{var}(LSM) = \mathrm{w}^2 \sum_{i-i_{\min}}^{i_{\max}} \frac{f_i(1-f_i)}{N_i - 1}, \qquad (9)$$

where N_i is number of individuals in the ith size class and the interval width (w) was constant.

The logistic regression (Cox and Snell, 1989) fits a logistic curve, ($\mu(a)$), the probability that a dolphin

Table 3

Age, length, corpus count, and reproductive condition for eight mature female *Delphinus delphis* taken in Japanese, Korean, and Taiwanese drift nets in the central North Pacific Ocean from February to December, 1990 and 1991.

Specimen number	Collection date	Length (cm)	Age (years)	Corpus count	Reproductive condition
RAT 036	23 Sep 90	170	10	1	Pregnant
EJW 037	25 Sep 90	172	8.5	3	Unknown
RAT 050	3 Oct 90	180	26	8	Resting
JAS 045	28 Mar 91	185	16.5	3	Pregnant
JAS 062	4 Jun 91	187	22.5	5	Resting
JAS 071	7 Jun 91	181	10	7	Lactating
JAS 109	26 Jun 91	177	26	6	Lactating
JAS 121	17 Jul 91	170	16.5	2	Resting

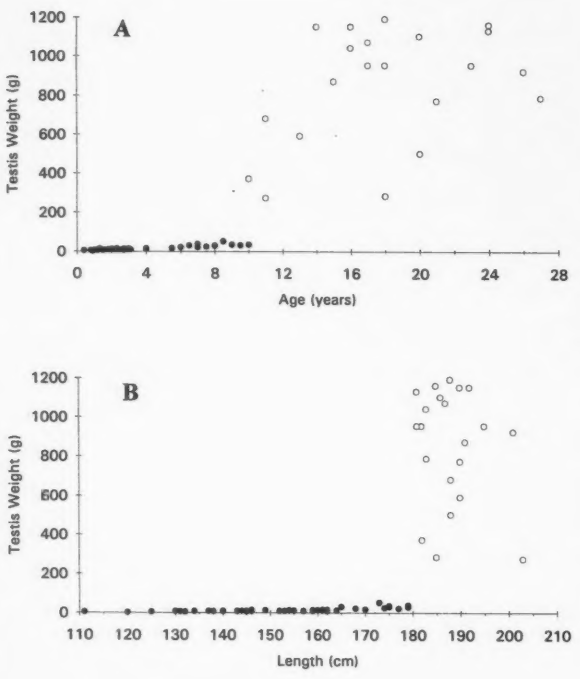

Figure 7

(**A**) Scatterplot of age (years) and testis weight (g) for 93 male common dolphin, *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean. (**B**) Scatterplot of length (cm) and testis weight (g) for 93 male *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

of length l is mature, to the distribution of mature and immature animals by age:

$$\mu = \frac{e^{1b+c}}{1+e^{1b+c}}, \tag{10}$$

where, l is the length of the dolphin and b and c are the slope and intercept of the regression. Average length at sexual maturation is then estimated as the age where $\mu(a) = 0.50$ so that LSM $= -c/b$.

The regression was done by using a maximum likelihood and iteratively reweighted least-squares algorithm (Chambers and Hastie, 1992). The standard error for μ was obtained by transforming the standard error of the linear fit.

Males Length at sexual maturation could only be suggested by the largest immature male, 179 cm, and the smallest mature male, 182 cm. There was a significant linear correlation between length and individual testis weight among immature animals (r^2=0.61, P<0.0001). Testis weights changed little with length up to the onset of sexual maturity when weights increased greatly (Fig. 7B). No correlation between length of mature animals and testis weights was detected (P>0.4).

Females Female average length at sexual maturation based on the DeMaster (1978) method was 172.8 cm (SE=0.56). With the logistic method, female LSM was 170.7 cm (SE=2.74). The smallest sexually mature female measured 170 cm; two corpora were present on the left ovary. The largest sexually immature female was 178 cm (Fig. 8B).

Ovulation rate Calculation of ovulation rate followed methods used for *Stenella attenuata* in Perrin et al. (1976). The average reproductive age ($\overline{A}$) in interval p was calculated as

$$\overline{A}_p = \frac{\left(\sum_i^p a_i b_i\right)}{c}, \tag{11}$$

where a is the percent maturing in the ith interval, b is the average reproductive age in interval p of females which matured in i, and c is the percent mature in interval p. The average corpus count in each age interval was calculated by dividing the sum of corpora counted in interval i by the number of mature females in interval i. We then regressed the average corpus count on the average reproductive age.

Ovarian scars numbered from 1 to 8 corpora among mature females. A linear model provided the best fit to the corpus count and average reproductive age data (r^2=0.61, P<0.1).

Seasonality Evidence of reproductive seasonality was detected by correlating age and length on collection date. From the aged portion of the sample we regressed ages of specimens ≤0.5 years (n=5) and the day of the year of collection using a linear model that resulted in the equation

$$y = 158.76 + 265.14x, \tag{12}$$

where x is age and y is the day of the year of collection. At age 0.0, the intercept corresponds to a date in early June, suggesting the calving mode. Both the slope and the intercepts were significant ($P<0.001$ and $P<0.05$, respectively).

We also regressed the lengths of specimens ≤115 cm from the overall sample ($n=30$) with day of the year. The 115-cm length corresponded to ages slightly older than 0.5 year for both sexes according to the predicted length-at-age relationship from the Laird/Gompertz growth model. We obtained the equation

$$y = -133.44 + 3.435x, \qquad (13)$$

where x is the length and y is the day of the year. Substituting 82 cm, our provisional length at birth, for x, the line intercepts a date in mid-May. Both the age- and length-based regressions suggest a seasonal peak in mid-May or early June. The lengths and dates of collection for the two fetuses also support this modal peak. The 65-cm fetus collected 28 March 1991 and the 12.6-cm fetus collected 23 September 1990 were projected to reach full-term in late May to early June.

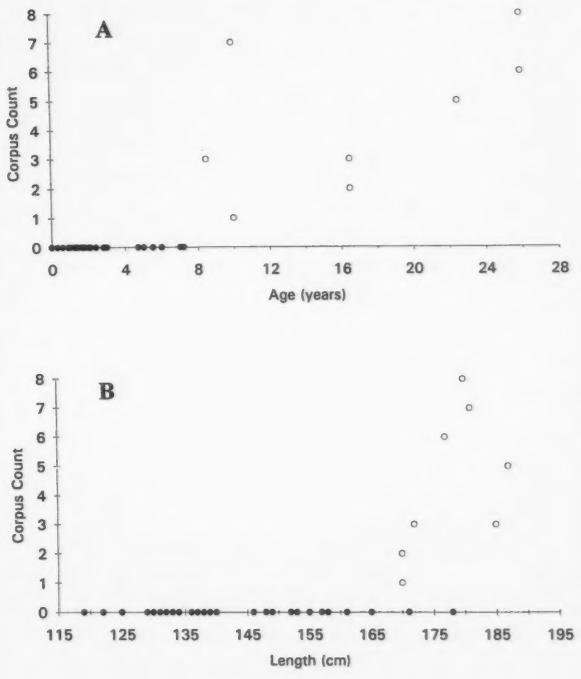

Figure 8

(**A**) Scatterplot of age (years) and total corpus count for 59 female, common dolphin, *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean. (**B**) Scatterplot of length (cm) and total corpus count for 59 female *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Discussion

The structure of the *D. delphis* sample suggested that it was suitable for preliminary estimation of several basic growth and reproduction parameters, although our values would be improved with larger sample sizes. With uncertain prospects for collecting additional *D. delphis* samples, owing to the discontinuation of the high seas squid driftnet fisheries and thus any associated sampling programs, we attempted to provide as much quantitative analysis as possible; however, we must regard many of our estimates as provisional. In particular, more reliable estimates of ASM and LSM will require more samples in the indeterminant age and length classes. Strong evidence of seasonality in calving made this sample unsuitable for calculation of calving interval, length of lactation, age of weaning, length of resting period, or reproductive rates.

Our application of the double Laird/Gompertz growth model is consistent with methods applied in previous growth studies on small cetaceans (Perrin et al., 1976, 1977), although our sample was not large enough to iteratively fit an intersection point between the upper and lower curves. While our application of the two-stage model suggests a secondary growth surge near the onset of sexual maturation, the magnitude and timing of that event should not be considered reliable without further sampling.

We attempted to fit a single Laird/Gompertz model to both the male and female data sets, but in both cases we encountered a preponderance of positive residuals at predicted lengths at age >10 years. Using the single curve, we predicted asymptotic lengths for both sexes at least 10 cm lower than any of the observed lengths for mature specimens. Our results from the double Laird/Gompertz model provide predicted length-at-age relationships with comparatively smaller residuals, distributed both positively and negatively at older ages.

Very few neonates, pregnant females with near-term fetuses, or lactating females, were collected even though we found strong evidence for a calving mode during the sampling period. We considered three possible factors to explain the inconsistency: 1) differing entanglement rates by various age and sex strata, 2) temporal disproportion in sampling effort, especially during the projected peak of the calving season, and 3) population segregation.

Following the same rationale developed for sampling *L. borealis* in Ferrero and Walker (1993), we did not consider the potential for bias as a result of the sampling method (i.e. incidental take in drift nets) to be a major factor. *Delphinus delphis* entanglements were scattered randomly along the length of the nets. Multiple entanglements were rare. The entanglements, therefore, appear to arise as individual events rather than as whole school encounters. Consequently, the sample likely reflects the composition of the population in the area rather than the composition of an individual school. There is also no evidence to assume that neonates or pregnant females avoid entanglement more than other age or sex strata.

Regarding the second possibility, the temporal distribution of the sample does not reflect low sampling effort during the late spring and early summer months. The peak in sampling effort occurred in June, and over 75% of that effort was accomplished in March–June. Thus, the absence of neonates and parturient females in the sample did not result from inadequate collection effort at that time.

Population segregation appears to be a likely factor in contributing to the small number of neonates and parturient females in our samples, and its effect is reflected in our sampling where collection locations tracked the northerly progress of the fishery. Our only advanced-term fetus was collected at the southern end of the study area in March. As the sampling effort moved northward, the parturient or lactating females and calves probably remained to the south and were unavailable for sampling. The remaining part of the female population appeared to have been represented in the sample.

The age and length distributions also reflect the likelihood that a significant portion of the female population was missing from the sample. The sex ratios calculated for specimens collected in areas south of lat. 34°N were not significantly different from 1.0; however, north of 34°N the ratio significantly differed from 1.0, favoring males in the 10 to 15 year-old age group. Furthermore, in the 15+ age group the sex ratio was not significantly different from 1.0 which is inconsistent with data for other delphinid species characterized by a greater proportion of mature females in the population (see Table 8 in Perrin and Reilly, 1984). Our age and length distributions, which suggest a male-dominated ratio, better describe only the part of the *D. delphis* population inhabiting the northern portion of the study area during the fishing season. These distributions and the sex ratio, therefore, should not be considered indicative of the overall population structure.

Schooling segregation by age, sex, and reproductive status has been demonstrated for numerous species of delphinid cetaceans (Perrin and Reilly, 1984); *Delphinus delphis* is among this group. Schooling segregation of *D. delphis* has been documented in the Black Sea where during calving and early lactation, females occur predominantly in offshore waters (Kleinenberg, 1956; Tomlin, 1957).

Our preliminary estimate of 11.1 months for gestation is similar to published accounts for the common dolphin. Gestation periods ranging from 10 to 11 months have been reported for *D. delphis* (Kleinenberg, 1956; Tomlin, 1957; Harrison, 1969).

Growth curves for North Pacific *D. delphis* have not been published and little definitive information on age and length at the onset of sexual maturation is available. Gurevitch and Stewart[3] reported that male *D. delphis* in the eastern tropical Pacific Ocean (central tropical population) reach sexual maturity around 6–7 GLG's, at a mean length of 200 cm. Hui (1979) presented data on *Delphinus* from southern California where females were reported to attain sexual maturity around 7–14 GLG's, and males between 8 and 12 GLG's. Length at onset of sexual maturation was 165–182 cm for females and 175–190 cm for males. Our preliminary estimates of age and length at sexual maturation for both sexes fall within the ranges presented in Hui (1979).

However, comparisons of our findings on the short-beaked *D. delphis* from the North Pacific transition zone with those from the southern California sample of Hui (1979) are potentially misleading, given recent evidence for the occurrence of two sympatric species of common dolphin in the southern California area (Heyning and Perrin, 1994). These two species, *D. bairdii* and *D. delphis*, are documented to differ markedly in overall size, and it is possible that Hui's (1979) sample contained members of both these species, accounting for the wide ranges in lengths at sexual maturation. In addition, differences in ages at onset of sexual maturation between our sample

[3] Gurevitch, V. S., and B. S. Stewart. 1978. Structure of kill of the common dolphin, *Delphinus delphis*, from the eastern tropical Pacific in 1977. Final Rep. for Contract 03-78-M02-0101, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038, 19 p.

and those presented in Hui (1979) and Gurevitch and Stewart[3] may be due to ageing methods. Both these studies employed an early technique of reading undecalcified, thin sections of formic-acid-etched teeth. This method is now considered imprecise for ageing small cetacean teeth (Perrin and Myrick, 1981).

Perryman and Lynn (1993) documented reproductive seasonality differences between three morphologically distinct common dolphin populations from adjacent but differing habitats in the eastern North Pacific Ocean. Calving season in the tropical region was year-round. In the temperate regions, which are characterized by a wider range of oceanographic conditions, strong evidence of reproductive seasonality was evident.

Our sample suggests evidence for a May–June calving peak as well as for schooling segregation of parturient females in the southern regions of the transition zone, closer to the subtropical domain. Evidence for pronounced reproductive seasonality should be anticipated in this region because the North Pacific transition zone is characterized by extreme oceanographic conditions, particularly in the northern regions adjacent to the subarctic frontal zone (Roden, 1991).

Acknowledgments

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The feasibility of direct photographic assessment of giant bluefin tuna, *Thunnus thynnus*, in New England waters

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Abstract.—Controversy concerning the validity and accuracy of recent assessment results for giant bluefin tuna, *Thunnus thynnus*, led us to examine alternative methods of estimating their abundance. In collaboration with a New England giant bluefin tuna industry group, we tested the feasibility of using commercial spotter pilots and aerial photography as a means of obtaining tuna counts in the Gulf of Maine and adjacent New England waters. Nine commercial spotter pilots photographed a total of 126 schools of bluefin tuna during the summer of 1993, representing 13,973 fish, with a maximum one-day count of 4,894. Three spotter pilots contributed nearly 70% of the total photographic effort. Differences in photographic ability and commercial involvement in the fishery appeared to influence spotter pilot participation. Aerial photographic surveys may provide a means of obtaining area-specific minimum abundance and distribution data for giant and large-medium bluefin tuna.

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Stock assessments of the highly migratory northern Atlantic bluefin tuna, *Thunnus thynnus*, are primarily based on age-structured and lumped biomass models derived from landings data and various abundance indices (Scott et al., 1993). These production or CPUE (catch per unit of effort) models provide the framework for international management of the commercially valuable bluefin tuna. A problem with CPUE-derived estimates of stock biomass, however, is that they are affected by changes in fishing effort, technology, fish density, and the marketplace (Lo et al., 1992). How accurately recent assessment models portray seasonal bluefin abundance in the west Atlantic, a fishery with a 1993 catch of 1,047.2 metric tons of giant tuna (≥77 inches straight fork length [SFL]) and of large-medium category tuna (between 70 and 77 inches SFL), remains controversial (Clay, 1991; Suzuki and Ishizuka, 1991; Safina, 1993).

Aerial surveys have been used to obtain relative indices of abundance in fisheries worldwide, including northern anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*), menhaden (*Brevoortia* spp.), mullet (*Mugil* spp.), and other pelagic fishes (Squire, 1961, 1972, 1993; Williams, 1981; Scott et al., 1989; Lo et al., 1992). Estimates of fish biomass from these surveys are based on appraisals of school size in tonnage per unit of area, or by size of remotely detected signals such as bioluminescence or turbidity fields. Visual biomass estimates from aerial survey data are relatively easy to construct but are difficult to interpret without ground truth or information on surfacing behavior (Lo et al., 1993).

In contrast, direct enumeration of pelagic fish is notoriously difficult. In the 1950's, U.S. fisheries scientists attempted to count giant bluefin tuna migrating along the Bahama Banks (Rivas, 1978) and later undertook direct assessment with photographic and video techniques (NMFS[1]). Despite dedicated search time, very few fish were detected during the survey. More recently, other countries have explored aerial and remote sensing methods as a means of calibrating catch-related indices for tuna species. Since 1990, transect surveys have provided estimates of regional abundance and recruitment indices for southern bluefin tuna, *Thunnus maccoyii*, in

[1] Anonymous. 1975. A study of the application of remote sensing techniques for detection and enumeration of giant bluefin tuna. Rep of Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA. Contrib. No. 437.

the Great Australian Bight (Morgan, 1992; Chen and Polacheck[2]). Aerial surface-detection radar surveys targeting bluefin tuna and other tunas have been explored by the French in the Mediterranean and tropical South Pacific areas (Petit et al., 1992).

Recently, members of the New England commercial giant bluefin tuna industry suggested that spotter pilots might provide a platform to examine the potential applications and limitations of direct visual assessment of giant and large-medium bluefin tuna. In coastal waters off New England, spotter pilots have located surface schools of giant bluefin tuna that are then targeted for capture by harpoon, hook and line, and purse-seine operations. In 1993, the New England Aquarium (NEA) and East Coast Tuna Association (ECTA) initiated a collaborative project involving fish spotter pilots locating and photographing surface schools of bluefin tuna normally targeted by the fishery. Our objective was to determine whether aerial photography could be used to provide information on the relative abundance, schooling characteristics, and spatial distribution of bluefin tuna.

Methods

The present study relied on a simple technical framework involving only voluntary participation by commercial spotters and the use of two cameras, one to photograph tuna schools (for enumeration) and another to document school location. Nine commercial spotter pilots participated in this survey while engaged in the 1993 seasonal fishery. All fish spotters flew single engine aircraft (models Cessna 172 and 182, Citabria, SuperCub) and were based on Cape Cod or in lower Maine. Four pilots spotted for seining operations, five were associated with harpoon or general category fishing (hook and line), and at least two participated in all three categories. Bluefin tuna were photographed from 23 July to 13 September, when participating pilots ceased activities because fishing quotas were filled.

Each pilot was provided with a hand-held 35-mm camera (Nikon N8008s) and an autofocus zoom lens (70–210 mm, F3.5/4.5, SIGMA Corp.) to photograph tuna schools. Synchronized databacks on cameras (Nikon, MF–21) imprinted date and time directly on exposed film. A second viewfinder camera (Shotmaster Ultra Zoom, 38–60 mm, f6.9 lens, Ricoh Corp.) was mounted overhead in the aircraft cabin to document positions from onboard global positioning system (GPS) or LORAN units located in or below the dashboard. Both cameras had auto advance features and were linked via cable so that they were simultaneously triggered when pilots depressed a remote shutter control. A photographic record of position (in TD Loran lines or lat./long.) could then be provided for each photographically documented tuna school. A digital clock synchronized with the 35-mm camera databack was mounted near the LORAN/GPS within range of the viewfinder camera. We could then verify sequence linkage between frames of tuna schools and locations if film advance speeds were not perfectly matched.

Tuna schools were photographed with color slide film (Ektachrome 400 ASA, Kodak), selected for depth of penetration and contrast characteristics (NMFS, 1975; Lockwood et al.[3]). Lenses were fitted with a circular polarizing filter or haze filter for glare reduction. Aircraft positions recorded by the viewfinder camera were read directly from developed black and white film (Tri-X 400 ASA, Kodak).

Pilots were supplied with labelled film canisters and with stamped and coded direct mailers for color processing, and were instructed to mail the film immediately when it was finished. Black and white film was returned directly to us and processed locally.

Analysis

Processed film was logged with an identification code, and a cursory examination was made on a light table with a film eye loupe. Tuna counts were made by projecting selected slides of schools and by visually counting individual fish. Images were enlarged by projection to a standard size (78 × 52 cm) onto a sheet of drafting-quality tracing paper marked with 10 × 10 cm square gridlines. Positions of clearly identifiable fish were marked and the total tallied per grid square and per slide frame. Upon completion of the tally, each sheet was labelled with the film identification code, frame number, time, and total fish count. No attempt was made to estimate the total number of fish in the school.

Since bluefin tuna are fast-swimming, mobile fish, it was possible for pilots to photograph the same school at slightly different locations on a single day. A school might be difficult to distinguish from adjacent, similarly sized schools. When photographed by a spotter in close succession, these schools had to have distinctly different spatial configurations or had

[2] Chen, S. X., and T. Polacheck. Data analysis of the aerial surveys (1991–1994) for juvenile southern bluefin tuna in the Great Austrialian Bight. 1994 SBT Recruitment Monitoring Workshop, Hobart, Tasmania. Available from T. Polacheck, CSIRO, Div. Fisheries, GPO Box 1538, Hobart, Tasmania 7001.

[3] Lockwood, H. E. Technicolor Graphics Services, Inc., Houston, TX 77058.

to be separated by at least one nautical mile (nmi) in order to be tallied independently. Spotters and fishermen reported maximum travel rates of 4–10 knots for bluefin tuna in the study area. With the assumption that swimming speeds were 10 knots, similarly sized schools photographed by different pilots on the same day had to be far enough apart so that it was unlikely that schools could have travelled from one location to the other in a given time period.

Results

The bluefin tuna survey area, fish spotter land bases, and locations of photographed schools are depicted in Figure 1. A total of 126 bluefin tuna schools, representing a cumulative count of 13,973 fish, were successfully photographed by spotter pilots on 17 days out of a 50-day survey period, for a total of 35 pilot-days. Pilots reported that, to the best of their knowledge, they photographed only giant or large-medium bluefin tuna size categories (>70 inches SFL), those targeted by the New England fishery. The position of surveyed schools, indicated by TD values or lat./long. on the pilot's navigational system, was established for 56 schools. Numbers of fish counted in schools ranged from 5 to 1,294 individuals (Fig. 2). Total giant and large-medium tuna counts were >1,000 fish on four survey days, with a maximum count of 4,894 tuna on 8 August (Table 1). A data summary of schools for three high count survey days (8–10 Aug) is given in Table 2.

From one to four spotters participated on high-count days, but no more than four pilots photographed fish on any given survey day. Spotters photographed schools from 0900 to 1803 h, but the greatest effort occurred during midday between 1200 and 1600 h (Table 3). Spotters report that slack tide (estimated to

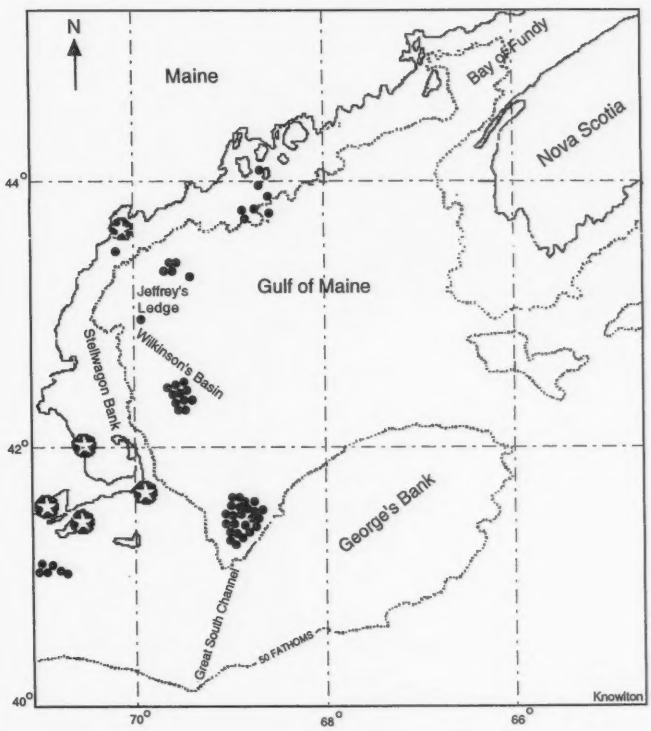

Figure 1

Aerial survey area for giant bluefin tuna, *Thunnus thynnus*, in New England waters, July–September 1993. Land bases of participating spotter pilots are indicated by stars. Filled circles indicate positions of photographed tuna schools.

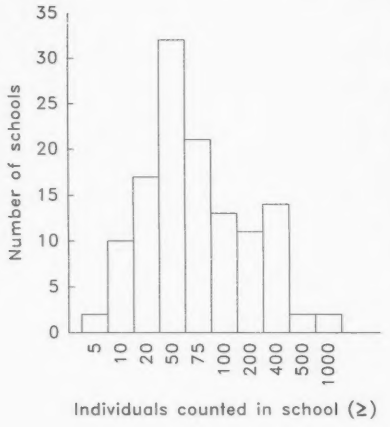

Figure 2

Frequency distribution of counts of giant and large-medium bluefin tuna, *Thunnus thynnus*, schools photographed by spotter pilots in New England waters, July–September 1993.

Table 1

Highest count days for aerial photography of bluefin tuna, *Thunnus thynnus*, in New England waters, July–September 1993.

Date[1]	Count	No. of schools	No. of pilots
8 Aug	4,894	24	2
22 Aug	2,517	16	4
9 Aug	1,067	15	2
10 Aug	1,275	7	1

[1] Full moon 2 August; new moon 17 August.

be within one hour of nearest coastal reference) often provides good conditions for locating fish. There was no discernible relation between lunar cycle or estimated slack tide and timing of greatest survey effort.

Surface schooling configurations of bluefin tuna, documented during the survey, included "soldiers" (small school of giants, fish swimming abreast in a parabola or straightline formation, Fig. 3A), "cartwheels" (spinning wheel-like formations, Fig. 3B), surface sheets (Fig. 3C), and densely packed domes (Fig. 3D). Basking sharks and, less frequently, humpback, fin, and other whales, were also photographed in association with bluefin tuna schools.

Discussion

Spotting and survey effort

Most of the bluefin tuna were photographed over a four-day period in August by only a few of the participating pilots, indicating that survey effort was strongly affected by environmental conditions and pilot effort. Fish spotters flew on less than half the survey period, grounded largely by inclement weather. They photographed all sizes of bluefin tuna schools, but small to medium-sized schools (≥5 counts <200) were located and photographed most frequently. Although initially instructed to document schools of any size, some pilots reported not bothering to photograph very small schools, particularly on "good" fishing days.

Search and photographic efforts of participating fish spotters varied widely, reflecting differences in commercial involvement in the fishery and in motivation. For example, one pilot photographed a minimum of 6,767 giant and large-medium bluefin tuna over five days under excellent survey conditions. However, his survey effort in hours represented <10% of the estimated 400 total flight hours he expended in the 1993 season. This result suggests that aerial photography of giant bluefin tuna can be accomplished with a small team of motivated pilots. In contrast, a fish spotter in partnership with seining operations photographed far fewer fish (467) because his total survey effort was limited to the few days permitted for his boat to achieve its seasonal quota. If all nine participating pilots had undertaken simultaneous surveys throughout the season, more complete documentation might have been achieved.

Throughout the survey we maintained frequent phone contact with the pilots in an effort to improve the quality of aerial and position photographs. Although we were able to count tuna in the majority of submitted frames, there was clearly a learning curve in the spotters' attempts to take high-resolution pictures. Blurring from aircraft vibration and underexposure were the most frequent problems with tuna school photographs. Unreadable Loran frames more often than not resulted from excessive glare on the digital readout, from improper film advance, or because the pilot had shifted position and had subsequently blocked the camera's view of the Loran. This problem could be eliminated if position were electronically logged each time the spotter photographed bluefin schools.

Enumeration analysis

In general, we assumed that environmental conditions were fairly uniform (low wind and sea states,

Table 2

Summary of photographed bluefin tuna, *Thunnus thynnus*, schools on three highest-count survey days in New England waters, July–September 1993.

Date	Pilot	Count	Time	Latitude (°N)	Longitude (°W)
08 Aug	g	57	12:53	41°25'	68°57'
08 Aug	g	152	12:59	41°25'	68°56'
08 Aug	g	186	13:01	41°25'	68°57'
08 Aug	g	284	13:09	41°25'	68°57'
08 Aug	g	1039	13:15	41°27'	68°55'
08 Aug	g	457	13:17	41°26'	68°57'
08 Aug	g	371	13:57		
08 Aug	f	96	14:09	42°27'	69°30'
08 Aug	g	26	14:27	41°28'	68°55'
08 Aug	g	499	14:28	41°28'	68°55'
08 Aug	g	315	14:37		
08 Aug	g	300	14:58	41°29'	68°55'
08 Aug	g	52	15:03	41°28'	68°56'
08 Aug	g	95	15:06		
08 Aug	g	42	15:09	41°29'	68°56'
08 Aug	g	85	15:17	41°28'	68°56'
08 Aug	g	107	15:31	41°29'	68°55'
08 Aug	f	313	15:34		
08 Aug	g	26	15:35		
08 Aug	f	85	15:45		
08 Aug	g	44	15:46		
08 Aug	g	69	15:54		
08 Aug	g	176	16:09	41°29'	68°55'
08 Aug	g	18	17:37	41°27'	68°57'
09 Aug	g	79	12:53		
09 Aug	g	60	12:58		
09 Aug	c	64	13:04		
09 Aug	g	83	13:12		
09 Aug	g	51	13:19		
09 Aug	c	22	13:20	4137	68°50
09 Aug	g	78	13:23		
09 Aug	g	94	13:40		
09 Aug	c	58	14:06	41°39'	68°44'
09 Aug	g	62	14:23	41°35'	68°45'
09 Aug	g	13	16:00	41°36'	68°47'
09 Aug	c	136	16:10	41°40'	68°42'
09 Aug	c	73	16:28	41°41'	68°41'
09 Aug	c	123	16:31	41°38'	68°40'
09 Aug	c	71	16:42	41°42'	69°03'
10 Aug	g	262	12:52	41°33'	68°48'
10 Aug	g	54	13:04	41°34'	68°48'
10 Aug	g	209	15:50	41°04'	70°51'
10 Aug	g	286	15:58	40°59'	70°47'
10 Aug	g	344	16:07	41°06'	70°56'
10 Aug	g	74	16:09	41°05'	70°56'
10 Aug	g	46	16:26	41°01'	71°02'

[1] Latitude and longitude have been rounded to nearest degree and minute.

good light levels, minimal glare) when schools were photographed. Altitude varied among spotters but seemed to be less important in producing good records than were sea state and light condition. However, spotters photographing large schools at low altitude were occasionally unable to include the entire school within the frame. We enumerated only clearly discernible individuals in schools and in some circumstances were able to count fish in at least one tier below the surface tier. With smaller schools, particularly in "soldier formation" or in surface-oriented groups, we were able to count all members of the school.

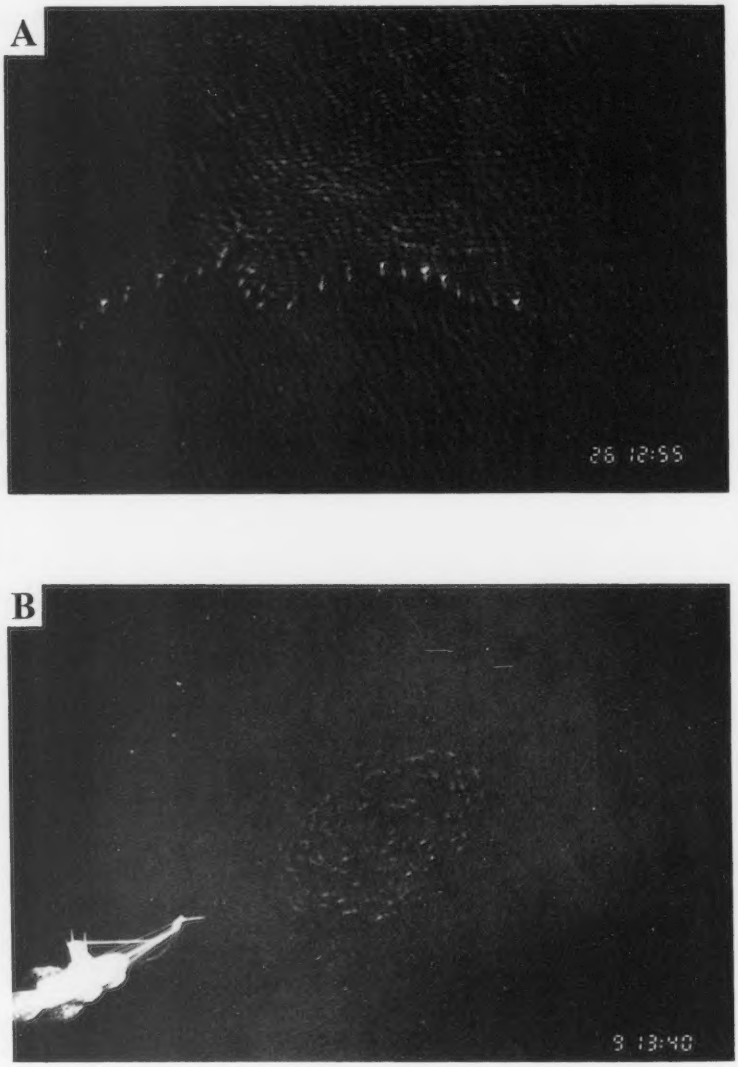

Figure 3

Examples of giant bluefin tuna school configurations photographed by fish spotters in the 1993 New England waters aerial census: (**A**) soldiers; (**B**) cartwheels; (**C**) surface sheet; and (**D**) densely packed dome.

Limitations of the data

Direct enumeration of giant bluefin tuna from aerial survey involves potential sources of error that must be addressed. These include species and size-class identification, differences in surfacing behavior caused by environmental or biological variables, and redundant counts as fish migrate through the study area. In the 1993 feasibility study, we identified and resolved only a few of these issues but nevertheless obtained information vital for improving future aerial surveys.

We observed small differences (<1%) in medium-size and large school totals when three different individuals examined and counted bluefin tuna in

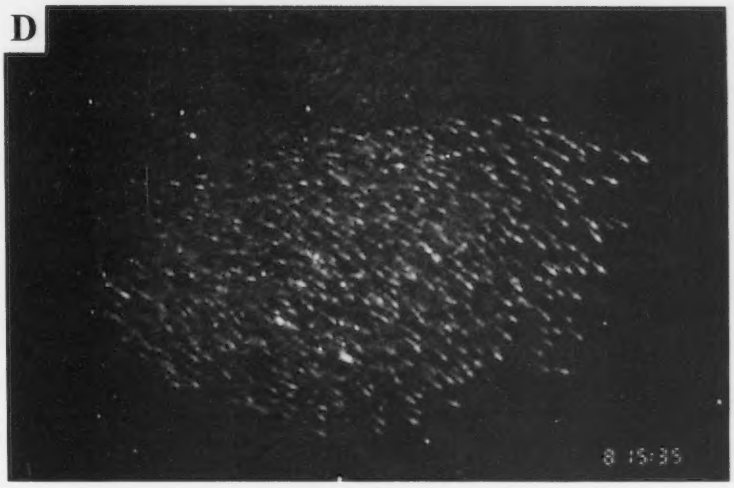

Figure 3 (continued)

projected images. Considering that we could enumerate only an undefined portion of the entire school, this source of error was considered negligible.

Species identification of small tunas by aerial observers can be difficult (Morgan, 1992), but the likelihood that spotters would mistake other species for giant or large-medium bluefin tuna targeted in this New England fishery is very slight. Commercially valuable schools of yellowfin tuna are rare north of Nantucket Shoals (Mather, 1962; Roffer, 1987), and experienced fish spotters would be unlikely to mistake targeted bluefin tuna for the smaller yellowfin tuna.

Marine mammals aggregate in groups of sizes comparable to that of giant bluefin tuna schools. Spotters have reported that they can easily distinguish giant and large-medium bluefin tuna from small marine mammals by body shape, tail orientation, and color, but identification is primarily made from swimming postures and frequency of dorsal flexure.

Table 3

Fish spotter photography effort by time of day in New England waters, July–September 1993.

Time of day (h:min)	No. of schools photographed
09:00–09:55	1
10:00–10:59	3
11:00–11:59	3
12:00–12:59	21
13:00–13:59	30
14:00–14:59	17
15:00–15:59	27
16:00–16:59	17
17:00–17:59	6
18:00–18:59	1

Because we did not have direct altimetry capabilities, size classes of bluefin tuna photographed in this survey could be generally documented only as large-medium or giants from spotter estimates alone. Spotters undoubtedly photographed, and we subsequently counted, some bluefin tuna below commercial size classes (<70 inches SFL). Catch records indicated that lengths of individuals in a school may vary by several inches, but only 10% of a seine catch is allowed to be undersized.[4] Because a spotter's survival in the commercial fishing industry depends upon size judgments being made before seine boats expend effort to capture schools, there is a strong selection for accuracy (Williams, 1981; Squire, 1993).

Despite confidence in spotter estimates (Squire, 1993), adequate documentation and validation of their ability to judge size or biomass are lacking. Research to define the accuracy of New England bluefin tuna spotter estimates, or to explore alternative methods of establishing lengths of photographed bluefin tuna, are clearly needed. Future surveys must obtain more specific information on size classes of photographed fish in order to be used as a point of reference for present CPUE-based models that use total length to assign year class (Anonymous, 1986).

The majority of bluefin tuna schools were photographed in five areas traditionally fished for giant tuna, including Great South Channel, Wilkinson Basin, Platt's Bank, and Jeffreys Ledge. This group of areas may reflect the past experience of the spotters and their unwillingness to search where fish are not usually found; it may also indicate that giant and large-medium-sized tuna exhibit clumped distributions in New England waters, where oceanic frontal systems, bottom topography, and concentration of prey provide favorable feeding and thermal conditions (Laurs et al., 1984; Maul et al., 1984; Roffer, 1987).

Clumped distributions make redundant counts an underlying problem for aerial assessments. Lacking GPS capabilities in 1993, we acknowledge that we may have counted bluefin tuna schools more than once because we had insufficient data to precisely locate all photographed schools. We have learned, however, that a given spotter is unlikely to photograph the same school twice over a period of a few hours. Once a spotter directs a boat onto a school, he moves to other areas because circling by boat is believed to force the fish down, rendering them difficult to catch for some time. In future surveys, an algorithm incorporating maximum swimming speeds and surfacing behavior could be used to limit redundant counts. Minimum counts based on daily rather than pooled totals would also reduce counting problems resulting from residence time and sequential movement of fish through the study area.

Conclusions

In this collaborative study neither we nor the ECTA believe that expended effort was sufficient to derive, on any given day, a minimum count of giant and large-medium bluefin tuna in New England waters. To do so would require not only perfect environmental conditions (noted by pilots and fishers as a "show" day) but also the complete cooperation and coordination of efforts by participating pilots. Given that the feasibility survey started relatively late in the fishing season, the latter was a difficult goal to achieve.

A fundamental limitation of aerial assessment is that only fish at or near the surface are accounted for, providing only a minimum estimate of school size. Surveyed schools subsequently captured by seiners might help define relations between aerial counts and total biomass, but this relation was established for only one set in the 1993 season. In this case (27 Aug), we counted 32 fish at the surface of a tightly domed school that yielded 125 large giants once captured.

Factors that govern schooling behavior and aggregation dynamics are poorly documented in bluefin tuna and the tunas in general (Mather, 1962; Clark and Mangel, 1979; Partridge et al., 1983). Mather (1962) described bluefin tuna behavior patterns of "pushing, milling, and smashing" in New England waters. We have noted spatial configurations (domes, cartwheels, surface sheets) and soldier groups (Partridge et al., 1983) depicted in photographed schools. Understanding the interplay of ecological and environmental factors that govern aggregation of giant bluefin tuna would help to define biases in direct assessment efforts. For example, giant bluefin tuna

[4] Foster, K. Gloucester Laboratory. Natl. Mar. Fish. Serv., NOAA, 30 Emerson Ave., Gloucester, MA 01930. Personal commun., March 1994.

are believed to exhibit the most rigidly defined spatial structures in schooling fishes (Partridge et al., 1983). If relations between the surface structure of schools and total biomass were known, surface counts could be adjusted to include an estimate of biomass.

In future studies, on-board data loggers might be used to give accurate records of search effort and survey tracks and possibly to determine fish size through direct altimetry from phototelemetry and GPS data. Hydroacoustic trials, Lidar, or remotely operated vehicle analysis undertaken alongside seining operations may provide additional groundtruth information that would allow derivation of indices of abundance (Petit et al., 1992).

In spite of limitations faced in the 1993 feasibility study, this preliminary aerial survey provided information on counts, distribution, and schooling characteristics of giant and large-medium bluefin tuna. Direct photographic surveys to obtain minimum counts of giant bluefin tuna may be a practical method of obtaining real-time measures of their relative abundance in New England waters.

Acknowledgments

This research was conducted under an agreement between the New England Aquarium and the East Coast Tuna Association (ECTA). The following pilots participated in data collection, served as the backbone of this survey, and provided valuable advice on fishery operations: Marc Avila, John Betzner, Wayne Davis, Jim Glyman, Roger Hillhouse, Ted Malley, Jonathan Mayhew, Norman St. Pierre, and Trip Wheeler. Richard Ruais, ECTA, and participating boat captains supported and funded the study and contributed organizational support. Grant MacNally served as photo consultant and helicopter pilot for film trials. We thank two anonymous reviewers for helpful comments on the manuscript.

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Egg and larval development of laboratory-reared gulf flounder, *Paralichthys albigutta*, and southern flounder, *P. lethostigma* (Pisces, Paralichthyidae)

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Abstract.—The egg and larval development of *Paralichthys albigutta* (gulf flounder) and *P. lethostigma* (southern flounder) are described from laboratory-reared and field-collected specimens. *Paralichthys albigutta* eggs and oil globules had a mean diameter of 0.87 mm (range: 0.84–0.90 mm) and 0.18 mm (range: 0.17–0.19 mm), respectively. *Paralichthys lethostigma* eggs and oil globules had a mean diameter of 0.91 mm (range: 0.84–0.96 mm) and 0.18 mm (range: 0.16–0.20 mm), respectively. Recently hatched *P. albigutta* larvae ranged from 1.8 to 2.2 mm in notochord length (NL) and *P. lethostigma* from 2.0 to 2.2 mm NL. Pigment on embryos and newly hatched larvae was relatively more developed for *P. albigutta*. Almost-paired and almost-contiguous ventral midline melanophores occurred on preflexion larvae of both species and remained throughout the larval stages. Pigment on the maxillary, vomer, dorsum of the mid-brain, lateral surface of the caudal area, lateral surface of gut, and extent of pigment along the ventral midline of the isthmus were used to separate laboratory-reared *P. albigutta* from *P. lethostigma*. However, this pigment was less useful in separating field-collected material. The number of cranial spines appeared to be diagnostic in separating laboratory-reared early-preflexion larvae. *Paralichthys lethostigma* consistently had three cranial spines, whereas *P. albigutta* had less than three spines. The development of meristic characters was considered the most useful character in separating *P. albigutta* from *P. lethostigma* because at any given size *P. albigutta* was generally more developed than *P. lethostigma*.

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Four species of the genus *Paralichthys* occur in southeastern U.S. coastal waters. *Paralichthys squamilentus* (broad flounder) is not commonly encountered and is of little commercial or recreational value. *Paralichthys dentatus* (summer flounder), *P. lethostigma* (southern flounder), and to a lesser extent *P. albigutta* (gulf flounder) are common and of great commercial and recreational value (N.C. Div. Marine Fisheries[1]). *Paralichthys dentatus* range from Maine to Cape Canaveral, Florida, and *P. albigutta* and *P. lethostigma* range from North Carolina to Texas (Gutherz, 1967). Eggs and larvae of *P. dentatus* have been described (Smith and Fahay, 1970) whereas those of *P. albigutta* and *P. lethostigma* have not. Comparative taxonomic studies of late larvae and early juvenile (fully formed vertebrae, dorsal, and anal rays) *P. dentatus*, *P. lethostigma*, and *P. albigutta* have been reported. Deubler (1958) showed that late-larval–early-juvenile *P. dentatus* can be distinguished from the other two congenera by differences in pigmentation of the dorsal and anal fins and in vertebral number. The only characters useful for separation of *P. lethostigma* and *P. albigutta* were dorsal-ray and anal-ray counts. Woolcott et al. (1968) showed that 100% separation of the three species could be obtained through a combination of anal-ray and vertebral counts. However, these characters must be fully formed in order to be diagnostic. Vertebral counts alone cannot be used to separate *P. albigutta* and *P. lethostigma*.

The objective of this study is to describe the eggs and larvae of laboratory-reared *P. lethostigma* and *P. albigutta* to provide diagnostic characters for identification of these paralichthyids in field-collected material.

[1] North Carolina Division of Marine Fisheries. 1992. Assessment of North Carolina commercial finfisheries. Completion Rep. for Job 2-IJ-16. North Carolina Div. Mar. Fisheries, Morehead City, NC 28557.

Methods

Adult *P. albigutta* and *P. lethostigma* were collected in the early fall during 1991 and 1992 from commercial pound nets in Core Sound, North Carolina. Individual fish were tagged and meristic data (gill-raker and anal-ray counts) were used to confirm identification (Gutherz, 1967). Spawning was induced with the aid of hormones as described by Smigielski (1975). For *P. albigutta* three different females were fertilized by a single male. Females were injected with carp pituitary hormone (2 mg/kg fish) two or three times to promote hydration. Eggs were fertilized on 14 and 19 February 1992. For *P. lethostigma*, a total of four different males and four different females were spawned. Eggs were fertilized on 17 December 1992, 24 February, and 2 March 1993.

Eggs and sperm from both species were manually stripped into 1-L bowls; eggs were fertilized, and embryos incubated in 100-L black-sided tanks. *Paralichthys albigutta* larvae were reared in uncirculated, filtered water at a mean temperature of 19°C (range: 14–24°C) and a mean salinity of 30 ppt (range: 28–30 ppt). *Paralichthys lethostigma* larvae were reared at a mean temperature of 18°C (range: 16–19°C) and a mean salinity of 32 ppt (range: 23–42 ppt). Rotifers and *Artemia* nauplii were provided to young (≤15 days old) and older (>15 days old) larvae, respectively. Only three *P. lethostigma* larvae were alive after approximately 35 days, limiting the amount of material available for this species. Eggs and larvae were preserved in 10% buffered formalin. Counts of meristic characters were obtained from cleared and stained specimens (Potthoff, 1984). All measurements and observations were made with a Wild M5A stereomicroscope equipped with an ocular micrometer.

The larval period was separated into preflexion, flexion, and postflexion stages—the three stages associated with the development of the caudal fin before, during, and after the upward flexion of the notochord tip. During preflexion and flexion, larval body length was measured from the tip of the snout to the tip of the notochord (notochord length, NL). In postflexion larvae (defined when 6 upper + 7 lower principal rays were formed) body length was measured from the tip of the snout to the base of the hypural plate (standard length, SL).

Postflexion larvae and transforming juveniles of *P. albigutta* and *P. lethostigma* captured in Onslow Bay off North Carolina during the winter of 1990 and 199l were used for 1) comparison with laboratory-reared specimens and 2) illustrations and investigation of pterygiophore patterns. This material also was used to determine the size when meristic characters develop for *P. lethostigma* because material from laboratory-reared specimens was limited for this species. Observations on pterygiophore patterns and meristic characters were made on cleared and stained specimens. Larval material is deposited at the Beaufort Laboratory under the care of the senior author.

Results

Eggs and recently hatched larvae

Paralichthys albigutta Eggs were spherical and had a mean diameter of 0.87 mm (range: 0.84–0.90 mm, n=44). One oil globule was present and had a mean diameter of 0.18 mm (range: 0.17–0.19 mm, n=44). The yolk was homogenous, the chorion smooth, and the perivitelline space (in live eggs) narrow (ca. 0.2 mm). Pigment was first observed in the caudal area of embryos just after blastopore closure (Fig. 1A). On embryos from late-stage eggs (from tail twisting to hatching), pigment occurred on the oil globule, sparsely in the head region, and was most

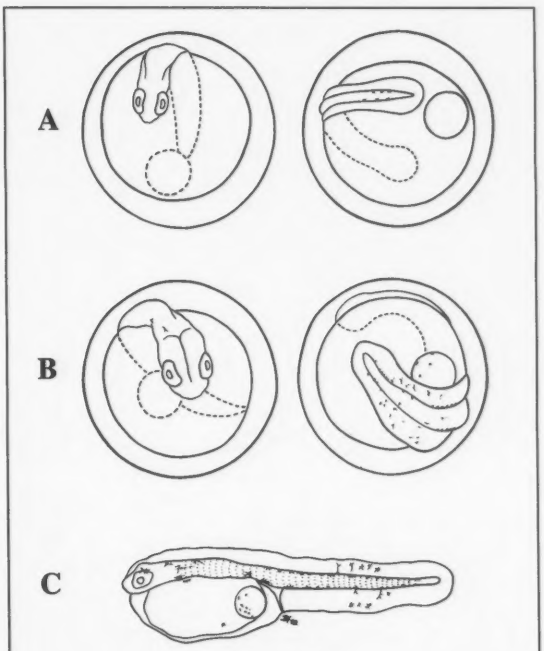

Figure 1

Laboratory-reared eggs and newly hatched larvae of gulf flounder, *Paralichthys albigutta*: (**A**) middle stage: left, anterior view; right, posterior view; (**B**) late stage: left, anterior view; right, posterior view; and (**C**) 2.2-mm-NL newly hatched yolk-sac larva.

developed in the caudal area. In the caudal area, melanophores occurred in the dorsal- and anal-fin folds, dorsal and ventral midlines, and sparsely on the lateral surface (Fig. 1B). Recently hatched *P. albigutta* larvae ranged from 1.8 to 2.2 mm NL. The oil globule was located in the posterior portion of the yolk sac (Fig. 1C).

Paralichthys lethostigma *P. lethostigma* eggs had a mean diameter of 0.91 mm (range: 0.84–0.96 mm, n=154), and the oil globule had a mean diameter of 0.18 mm (range: 0.16–0.20 mm, n=154). Pigment on embryos from middle-stage eggs (just after blastopore closure) was less developed than that observed for *P. albigutta* (Fig. 2A). Like *P. albigutta*, pigment on *P. lethostigma* embryos was only observed in the caudal area. Pigment on embryos from late-stage eggs was less developed than that observed for *P. albigutta* (Fig. 2B). Pigment was observed only in the caudal area on *P. lethostigma* embryos. Recently hatched *P. lethostigma* larvae were similar in size to *P. albigutta* (range: 2.0–2.2 mm NL). Like *P. albigutta*, the oil globule was located in the posterior portion of the yolk sac (Fig. 2C).

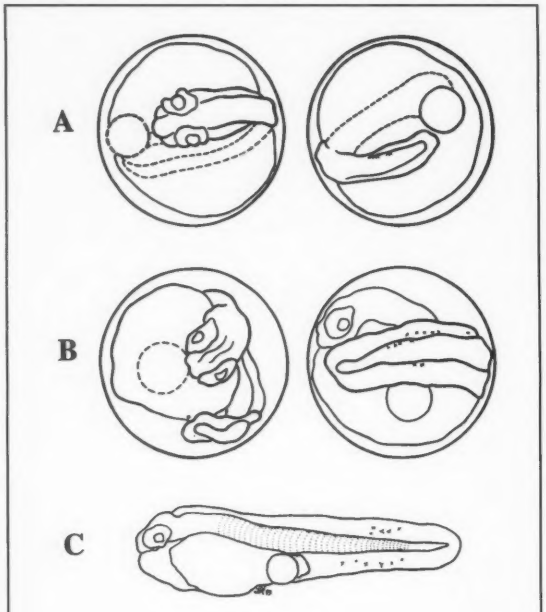

Figure 2

Laboratory-reared eggs and newly hatched larvae of southern flounder, *Paralichthys lethostigma*: (**A**) middle stage: left, anterior view; right, posterior view; (**B**) late stage: left, anterior view; right, posterior view; and (**C**) 2.1-mm-NL recently hatched yolk-sac larva.

Fin development

Paralichthys albigutta Fins began to develop in the following sequence: dorsal and caudal, anal, pelvic, and pectoral (Table 1). The adult complement of rays (Gutherz, 1967; Woolcott et al., 1968; Fahay, 1983) was attained in the following sequence: principal caudal rays (10 upper + 8 lower), dorsal fin (71–85), anal fin (53–63) and pelvic fin (6), and pectoral fin (10–12) (Table 1).

The development of the caudal fin, indicated by a thickening of tissue on the ventral side, began at 5.2 mm NL. Caudal-fin rays (2 upper + 2 lower) were first observed at 5.5 mm NL, indicating the beginning of the flexion stage. The rays began to form at the middle of the fin and developed dorsally and ventrally almost simultaneously. The adult complement of principal caudal rays (10 upper + 8 lower) was attained at 6.9 mm SL.

Dorsal rays were first observed during early flexion (5.5 mm NL, Table 1). Dorsal rays first formed in the head region anterior to the first neural spine. They were accompanied by an extension of the dorsal-fin fold that appeared as a flap (Fig. 3B). Dorsal-fin development proceeded slowly during the flexion stage and more rapidly during postflexion (Table 1). Development proceeded posteriorly; however, the anteriormost ray was not observed until 6.1 mm SL. The anterior rays in the head region, especially the third ray, were elongated (Fig. 3D). The adult complement of dorsal-fin rays consistently was attained at 7.8 mm SL (Table 1).

Anal-fin rays began to form on postflexion larvae at approximately 6.1 mm SL (Table 1). Formation began in the vicinity of the first haemal spine and development proceeded anteriorly and posteriorly simultaneously. Anal-fin-ray development was rapid, and by 7.7 mm SL the adult complement of anal-fin rays consistently was observed (Table 1).

Pelvic-fin rays were first observed on postflexion *P. albigutta* larvae at 6.9 mm SL (Table 1). All specimens ≥8.5 mm SL had a completed pelvic fin.

The pectoral fin persisted as a large rayless blade throughout flexion and early postflexion (Table 1). Rays began to form at 7.1 mm SL at the dorsal position of the blade and developed ventrally (Fig. 4). All specimens ≥8.5 mm SL had the adult complement (10–12 rays) of pectoral fin rays (Table 1).

Paralichthys lethostigma Fins began to develop in the following sequence: dorsal, caudal, anal, pelvic and pectoral (Table 2). The adult complement of rays (Gutherz, 1967; Wolcott et al., 1968; Fahay, 1983) was attained in the following sequence: caudal fin (10 upper + 8 lower), dorsal fin (80–95) and anal fin (63–74), pelvic fin (6), and pectoral fin (11–13) (Table 2).

Table 1

Meristic data from cleared and stained laboratory-reared gulf flounder, *Paralichthys albigutta*. Dashed lines separate preflexion, flexion, and postflexion stage larvae. Postflexion was defined as the stage when 6 upper + 7 lower caudal rays were observed. NL = notochord length; SL = standard length.

Body length (mm)	Days after hatching	Dorsal-fin rays	Anal-fin rays	Pelvic-fin rays	Pectoral-fin rays	Principal caudal rays (upper + lower)
4.5 NL	18	0	0	0	0	0
5.2 NL	19	0	0	0	0	0
5.5 NL	19	3	0	0	0	2+2
5.7 NL	19	2	0	0	0	2+2
5.7 NL	19	2	0	0	0	2+2
5.8 NL	19	3	0	0	0	3+3
5.8 NL	24	5	0	0	0	6+5
6.1 NL	19	2	0	0	0	3+3
6.4 NL	31	4	0	0	0	5+5
5.9 SL	24	9	0	0	0	7+7
6.1 SL	26	15	4	0	0	9+8
6.3 SL	26	16	14	0	0	9+8
6.8 SL	31	55	34	0	0	9+8
6.9 SL	36	72	54	3	0	10+8
7.0 SL	36	68	50	4	0	10+8
7.1 SL	36	68	50	5	1	10+8
7.2 SL	31	62	43	0	0	10+8
7.7 SL	36	74	57	5	3	10+8
7.8 SL	36	69	54	5	5	10+8
7.8 SL	44	75	54	5	9	10+8
8.0 SL	36	72	55	5	5	10+8
8.2 SL	44	72	51	5	5	10+8
8.5 SL	44	71	54	6	10	10+8
8.6 SL	44	74	56	6	10	10+8
10.2 SL	59	74	58	6	11	10+8
10.7 SL	52	73	54	6	13	10+8

The development of the caudal fin began at 5.4 mm NL and was similar to that of *P. albigutta*, but caudal rays were not observed until 6.5 mm NL. The adult complement of principal caudal rays (10 + 8) was attained at 8.2 mm SL (Table 2).

Dorsal rays were first observed on a preflexion specimen but were not consistently observed till early flexion (6.5 mm NL, Table 2). The development of dorsal rays was similar to that observed for *P. albigutta*. Complete development of the dorsal-fin rays occurred at approximately 8.4 mm SL.

Anal-fin rays began to form on postflexion larvae at approximately 7.3 mm SL. Development was similar to that observed for *P. albigutta*. Like *P. albigutta*, anal-fin-ray development was rapid and the anal fin appeared to be completely formed by approximately 8.4 mm SL (Table 2).

Pelvic-fin rays were first observed on postflexion larvae (8.2 mm SL, Table 2). All specimens >9.7 mm SL consistently had a completed pelvic fin.

Pectoral-fin rays began to form at 8.4 mm SL at the dorsal position of the blade and developed ventrally. The largest specimen (11.0 mm SL) still had not attained a completed (11–13 rays) pectoral fin (Table 2).

Pigmentation of laboratory-reared specimens

Paralichthys albigutta Newly hatched *P. albigutta* larvae had dendritic melanophores on the dorsal and anal finfolds midway between the anus and notochord tip (Fig. 1C). Dorsal and anal midline pigment posterior to the anus was well developed. Melanophores occurred on the trunk and head, on the oil globule, and on the yolk sac (Fig. 1C). Melanophores were observed on the snout on a one-day old larva (2.8 mm NL) but not on newly hatched larvae.

Characteristic pigment on preflexion larvae was almost-paired and almost-contiguous dorsal and ventral midline melanophores that remained character-

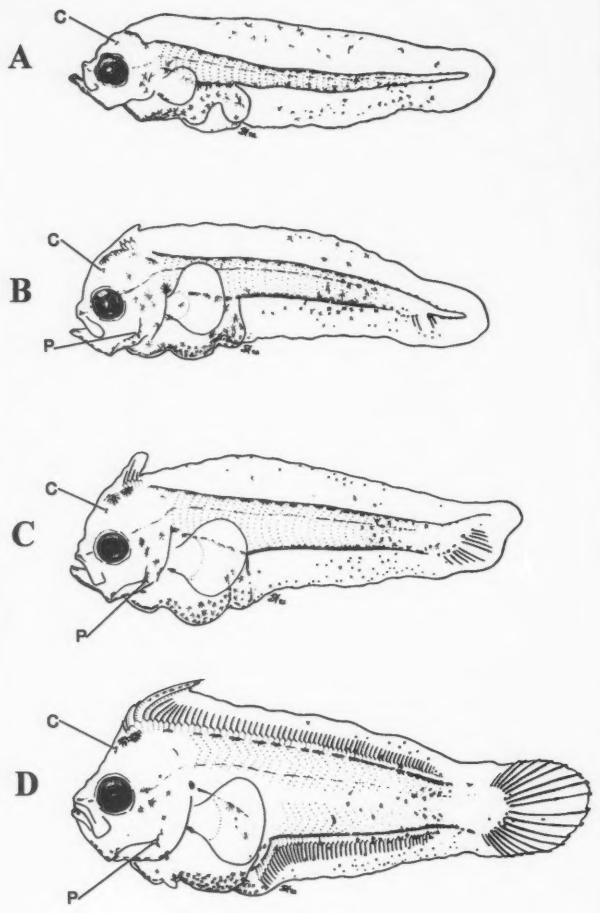

Figure 3

Developmental stages of laboratory-reared gulf flounder, *Paralichthys albigutta* (C=cranial spines, P=preopercular spines). (**A**) 3.5-mm-NL preflexion larva, 10 days old; (**B**) 5.8-mm-NL early flexion larva, 25 days old; (**C**) 6.2-mm-NL late flexion larva, 21 days old; and (**D**) 7.1-mm-SL postflexion larva, 31 days old.

istic throughout the larval stages (Fig. 3A). The almost-paired dorsal and ventral midline melanophores merged into one row of dorsal and ventral punctate melanophores in the future caudal-fin region. The most posterior melanophores generally were opposite each other. The dorsal midline pigmentation extended anteriorly to the forebrain. Melanophores were first observed on the lateral portion of the caudal region at approximately 3.5 mm NL (Fig. 3A). Embedded notochord pigment extended anteriorly ventral to the brain and continued through the eye, giving the appearance of a stripe through the eye. Pigment occurred over most of the ventral finfold and more prevalently in the middle one-third of the dorsal finfold. In the gut region of preflexion larvae, melanophores occurred along the ventral midline, extending anterior of the cleithral symphysis and along the lateral surface of the gut. Melanophores occurred along the dorsal surface of the gut as a continuation of ventral midline pigment and generally terminated in a distinct melanophore at the junction of the operculum (Fig. 3A). In most specimens a distinct melanophore occurred on the ventral area of the base of the pectoral-fin blade. In the head region, melanophores occurred on the operculum and on the dorsum of the midbrain (cranial bump). Pigment was first observed on the dorsum of the cranial bump during early preflexion (2.9 mm NL), but only 20% of the specimens examined (n=10) had a melanophore here at this time. With increasing size the cranial-bump melanophore occurred at a greater frequency, and by 4.0 mm NL all specimens had a melanophore in this region. In the lower-jaw region, melanophores occurred both along the lower-jaw rami and at the lower-jaw angle (Fig. 3A). A punctate melanophore was observed on both sides of the premaxilla or maxilla, or both. This pair of melanophores was first observed on early preflexion larvae (2.9 mm NL) and was observed on every laboratory-reared specimen examined. Vomerine pigment was first observed on 3.2-mm-NL preflexion larvae and occurred thereafter on all specimens examined.

Pigment on flexion larvae was similar to that observed on late preflexion larvae (Fig. 3, B and C). Melanophores occurred on the lateral surface of the body in the caudal area on all specimens. The most anterior melanophore on the dorsal surface of the gut at the junction of the operculum was stellate and was seemingly isolated from the other gut pigmentation (Fig. 3, B and C). Pigment occurred along the proximal base of the developing caudal-fin rays. In the late flexion stage (6.4 mm NL), pigment first appeared on the third elongated dorsal ray. Most of the lateral surface of the hind gut was pigmented. The ventro-lateral surface of the mid- and foregut was pigmented (Fig. 3, B and C).

On early postflexion larvae (Fig. 3D), pigment was observed on the base of the caudal fin and on the

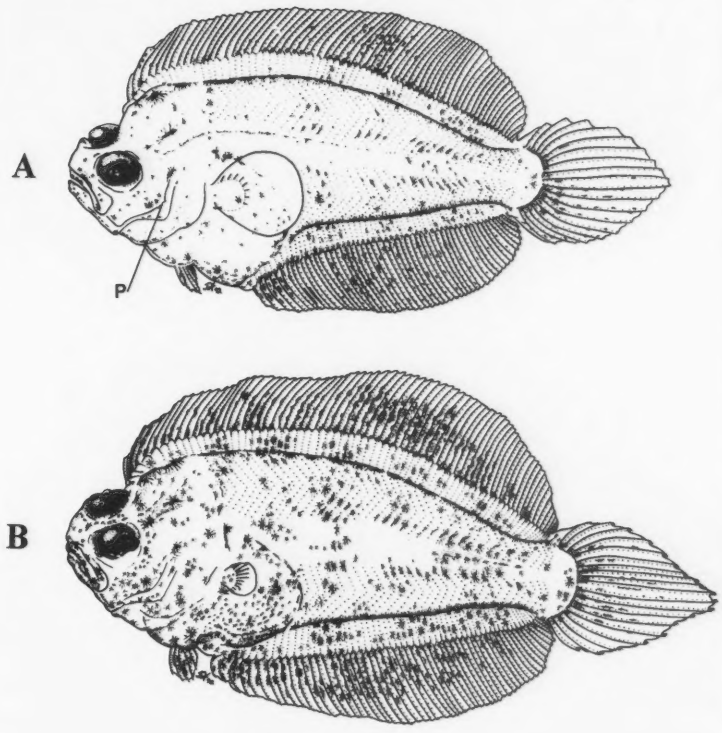

Figure 4

Developmental stages of transforming, postflexion laboratory-reared gulf flounder, *Paralichthys albigutta* (P=preopercular spines). (**A**) 8.2-mm-SL larva, 34 days old; (**B**) 9.0-mm-SL larva, 45 days old.

pelvic fin. Melanophores on the lateral surface of the body in the caudal area began to align with the myosepta. Pigment on the lateral surface of the body increased with increasing size (Fig. 4). The extended third dorsal ray was pigmented, and pigment was scattered on the developing dorsal- and anal-fin rays. This pigment increased in area during development (Fig. 4). Pigment was scattered in no apparent pattern medially on the dorsal- and anal-fin pterygiophores. The anal-fin pterygiophores were relatively more pigmented than those on the dorsal fin. Pigment increased in these areas during development (Fig. 4). The characteristic almost-paired, almost-contiguous dorsal and ventral midline pigment was located at the proximal edge (base) of the dorsal- and anal-fin pterygiophores. Pigment in the head region of early postflexion larvae was similar to that of flexion larvae (Fig. 3D) but increased in intensity during development (Fig. 4).

During transformation, *P. albigutta* larval body pigment increased in intensity (e.g. compare Fig. 4, A and B). Melanophores occurred along the entire base of the caudal fin, but most of the fin was not pigmented. A blotchy pigment pattern was observed on the pterygiophores, caudal peduncle, and lateral line from mid-body anterior to the cleithrum. Melanophores along the lateral line from mid-body to the caudal peduncle formed a streak of pigment in later transforming larvae (ca. 8.7 mm SL). Numerous melanophores on the lateral surface of the caudal area were aligned with the myosepta. This pigment occurred mainly in the posterior two-thirds of the caudal area and extended more anteriorly in the dorsolateral area (Fig. 4). The dorsal and anal fins were pigmented along the entire length of their base (i.e. proximally). On the medial portion of the dorsal- and anal-fin rays on earlier (ca. 7.8 mm SL) transforming larvae, pigment appeared as blotches on the

Table 2

Meristic data from cleared and stained laboratory-reared and field-collected southern flounder, *Paralichthys lethostigma*. Dashed lines separate preflexion, flexion, and postflexion stage larvae. Postflexion was defined as the stage when 6 upper + 7 lower caudal rays were observed. An asterisk indicates field-collected material. NL = notochord length; SL = standard length.

Body length (mm)	Days after hatching	Dorsal-fin rays	Anal-fin rays	Pelvic-fin rays	Pectoral-fin rays	Principal caudal rays (upper+lower)
4.7 NL	20	0	0	0	0	0
4.9 NL	20	0	0	0	0	0
5.4 NL	20	0	0	0	0	0
6.2 NL	31	2	0	0	0	0
6.4 NL	24	0	0	0	0	0
6.5 NL	31	6	0	0	0	5+5
6.6 NL	31	5	0	0	0	4+4
6.8 NL	31	4	0	0	0	4+3
6.9 NL	31	5	0	0	0	6+6
6.9 NL	35	6	0	0	0	6+6
7.0 NL	40	5	0	0	0	5+5
7.1 NL	35	6	0	0	0	6+6
6.7 SL	39	13	0	0	0	7+8
6.7 SL	*	13	0	0	0	9+8
6.7 SL	*	10	0	0	0	9+8
7.3 SL	*	14	13	0	0	7+6
7.3 SL	48	9	0	0	0	7+8
7.8 SL	*	68	41	0	0	9+8
8.2 SL	*	84	65	5	0	10+8
8.4 SL	*	90	71	5	2	10+8
8.7 SL	*	90	70	5	2	10+8
9.2 SL	40	82	62	6	0	10+8
9.2 SL	*	83	64	6	5	10+8
9.7 SL	*	85	67	5	1	10+8
9.8 SL	*	87	63	6	2	10+8
9.8 SL	*	87	65	6	4	10+8
10.2 SL	*	85	64	6	6	10+8
11.0 SL	*	86	63	6	9	10+8

anterior and midbody surfaces of the fins and gradually expanded over the medial portion with development (Fig. 4).

Paralichthys lethostigma Newly hatched *P. lethostigma* larvae had melanophores on the dorsal and anal finfolds that were concentrated in the middle of the body (Fig. 2C). Dorsal midline pigment was well developed and generally occurred from the anterior portion of the caudal region to the head and snout. There were fewer melanophores on the dorsal and ventral midline posterior to the anus (i.e. in the caudal region). Pigment was observed on the oil globule.

Like *P. albigutta*, characteristic pigment on *P. lethostigma* preflexion larvae was almost-paired and almost-contiguous dorsal and ventral midline melanophores that merged into one row of dorsal and ventral melanophores in the future caudal-fin region (Fig. 5A). On very early preflexion larvae (2.8–3.0 mm NL) that still contained vestiges of yolk and oil, the dorsal midline melanophores were continuous over the brain and snout, and the ventral midline melanophores were continuous over the gut. Melanophores on the lateral portion of the caudal region were not observed on early preflexion larvae (ca. <3.6 mm NL) and were not as well developed on later preflexion larvae compared with *P. albigutta* larvae (Figs. 3A and 5A). In the gut region of preflexion *P. lethostigma*, the lateral portion of the gut was typically devoid of pigment (Fig. 5A) and was never as well developed as that observed for *P. albigutta* (Fig. 3A). Usually, ventral melanophores in the gut region

were not continuous because a gap appeared just anterior to the anus. Regularly, we observed a pair of melanophores located ventrally on each side of the hindgut. The pectoral-fin-ray blade was pigmented. Pigmentation of preflexion *P. lethostigma* at the base of the pectoral fin and in the head region was similar to that observed for *P. albigutta* (Figs. 3A and 5A). Pigment on the maxillary and the dorsum of the midbrain (cranial bump) was less frequently observed in preflexion *P. lethostigma* larvae compared with preflexion *P. albigutta* larvae. Cranial bump pigment was observed on 36% of the specimens and maxillary pigment on 64% of the specimens (n=25). Pigment on the vomer of preflexion *P. lethostigma* also occurred less frequently (36% of the specimens had this pigment; n=15); however, this pigment was difficult to discern. It was most effectively seen on fresh, cleared and stained material. Ventral pigment on the isthmus, anterior to the cleithrum, did not extend the full length of the isthmus as was observed on preflexion *P. albigutta* (Figs. 3A and 5A). The number of melanophores observed on the operculum (commonly one) was less than that observed for *P. albigutta*.

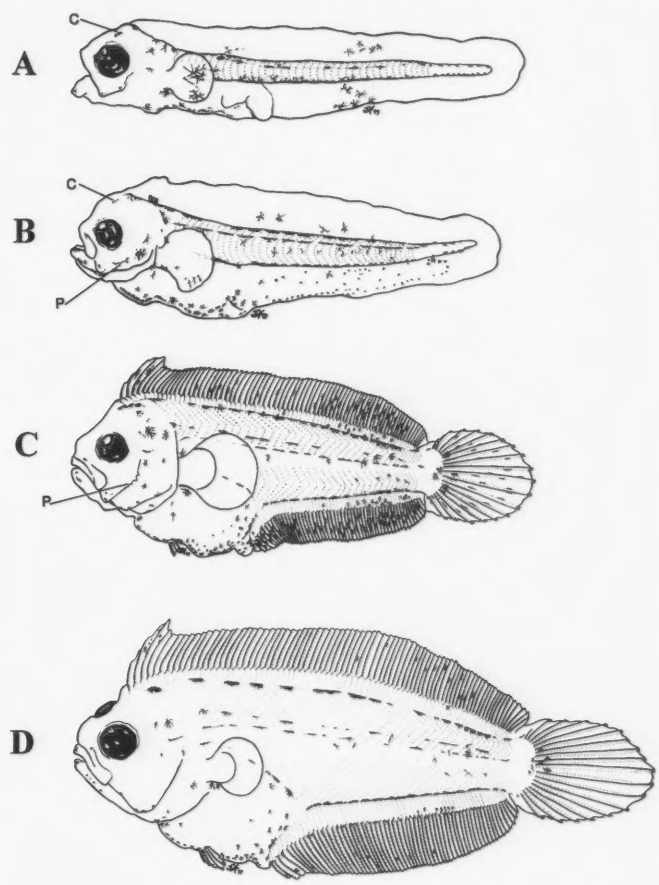

Figure 5

Developmental stages of laboratory-reared southern flounder, *Paralichthys lethostigma* (C=cranial spines, P=preopercular spines). (**A**) 3.3-mm-NL early preflexion larva, 9 days old; (**B**) 6.4-mm-NL late preflexion larva, 24 days old; (**C**) 7.7-mm-SL postflexion larva, 45 days old; and (**D**) 9.1-mm-SL transforming postflexion larva, 40 days old.

Pigment on flexion *P. lethostigma* larvae was similar to that observed on later preflexion larvae (Fig. 5B). Melanophores were observed on the lateral side of the caudal region; however, they were less organized than those observed for *P. albigutta*, which appeared to be more banded in appearance. During flexion, pigmentation increased on the lateral surface of the hindgut. Dorsal finfold pigmentation was sparse and located at midbody. Ventral finfold melanophores occurred along the distal margin and on the finfold surface at midbody. A melanophore was observed at the ventral edge of the pectoral-fin blade, and a distinct melanophore was observed at the junction of the dorsalmost portion of the opercle and the anteriodorsal portion of the gut. This characteristic pigmentation was observed for both species. Pigmentation along the ventral midline of the isthmus increased to cover the entire isthmus. Like *P. albigutta*, melanophores were typically observed on the maxillary and the dorsum of the midbrain, but vomerine pigment was irregularly observed on flexion *P. lethostigma* larvae. Pigmentation (1–4 melanophores) occurred on the opercular region posterior to the eye. Melanophores along the edge of the interopercle and subopercle were first observed on flexion larvae.

On postflexion larvae (6.4–9.3 mm SL), pigment was observed at the base of the caudal fin and on the pelvic fin (Fig. 5, C and D). Melanophores occurred on the lateral surface of the body, but they were never

aligned with the myosepta as was observed for *P. albigutta* (Figs. 3D, 4, and 5).

Other structures and size at transformation

Dorsal and anal fin supports The arrangement of pterygiophores in relation to neural and haemal spines may be valuable for separating *P. albigutta* and *P. lethostigma* larvae because they share similar vertebral counts (hence similar haemal and neural spine counts), but different dorsal and anal fin-ray counts.

The cumulative number of anal-fin-ray pterygiophores between the first haemal spine (which is associated with the first caudal vertebrae) and haemal spines posterior to the fourth haemal spine appeared to be diagnostic (Table 3). Although there was overlap in counts, there is a fair degree of separation in the cumulative number of anal-fin pterygiophores. For example, between haemal spines 1 and 13, from 28 to 31 pterygiophores would aid in identifying *P. albigutta*, whereas ≥28 pterygiophores would aid in identifying *P. lethostigma*. As expected, there was a lesser cumulative number of pterygiophores for *P. albigutta* compared with *P. lethostigma* (Table 3).

The cumulative number of dorsal-fin pterygiophores between the first neural spine (which is associated with the first caudal vertebrae) and following spines appeared less valuable (Table 3). There was considerable overlap between species. The cumulative number of pterygiophores was most valuable when a considerable number were developed. For example, between neural spines 1 and 27, from 46 to 52 pterygiophores would aid in identifying *P. albigutta*, whereas ≥58 pterygiophores would aid in identifying *P. lethostigma* (Table 3).

Cranial spines and preopercle spines Weak, fleshy preopercle spines were observed on both species at all stages, and they decreased in number with increasing size (Figs. 3–5). On both species the exact arrangement and number of preopercle spines generally were difficult to discern but were more readily observed in cleared and stained material. Generally, there were four to five minute spines on the inner shelf of the preopercle, a larger spine at the angle of the outer shelf, and one dorsal to the latter on the outer shelf. Preopercle spines were not observed for specimens of either species ≥ approximately 8.5 mm SL.

Cranial spines may be diagnostic for separating *P. albigutta* and *P. lethostigma* preflexion larvae. We consistently observed three cranial spines on *P. lethostigma* preflexion larvae (2.9–5.4 mm NL). We never observed more than two (zero to two) on *P. albigutta* preflexion larvae of similar size. However, in most instances spines could be discerned only on cleared and stained material. Cranial spines generally were never observed on postflexion larvae of either species.

Paralichthys albigutta began transformation at a smaller size than did *P. lethostigma*. For *P. albigutta*, the migrating eye first appeared at the dorsal midline at 7.8 mm SL. On all specimens >7.8 mm SL, the eye had migrated at least to the dorsal midline. For *P. lethostigma*, the migrating eye first appeared at the dorsal midline at 8.7 mm SL. With one exception, the eye had migrated to at least the dorsal midline on all larvae >8.7 mm SL. On one field-collected larva of 11.2 mm SL, the eye had barely reached the dorsal midline as described for *P. dentatus* (Fahay, 1983). Pigmentation and meristic characters clearly identified this specimen as *P. lethostigma*.

Table 3

The cumulative number (range) of pterygiophores between the first neural and haemal spines and other spines (up to neural and haemal spine number 30 and 20, respectively) for gulf flounder, *Paralichthys albigutta* (*n*=15 laboratory-reared and 14 field-collected specimens) and southern flounder, *P. lethostigma* (*n*=1 laboratory-reared and 13 field-collected specimens).

Spine numbers	*P. albigutta*		*P. lethostigma*	
	Dorsal fin	Anal fin	Dorsal fin	Anal fin
1–2	2–3	1–3	2–3	2–3
1–3	4–6	3–5	5–6	4–5
1–4	5–8	5–7	7–9	6–8
1–5	6–9	7–9	8–9	9–10
1–6	8–10	9–11	8–10	11–13
1–7	9–12	10–13	10–12	13–16
1–8	11–13	12–15	12–14	15–18
1–9	13–16	14–17	14–16	17–21
1–10	15–18	16–20	16–18	19–23
1–11	16–21	17–22	18–21	22–26
1–12	18–23	19–25	20–23	24–29
1–13	20–25	21–27	23–26	26–31
1–14	22–28	23–29	25–29	28–34
1–15	24–30	25–31	27–31	30–37
1–16	26–33	27–33	30–34	33–39
1–17	28–35	29–36	32–36	34–42
1–18	30–37	31–38	34–38	37–45
1–19	32–40	33–40	36–41	39–48
1–20	34–42	36–42	38–43	43–51
1–21	36–44		40–45	
1–22	38–46		42–48	
1–23	39–49		44–50	
1–24	41–51		46–53	
1–25	43–53		48–55	
1–26	45–55		51–58	
1–27	46–57		53–61	
1–28	48–60		55–64	
1–29	51–62		58–67	
1–30	53–65		60–70	

Identification of field-collected material Material collected from Onslow Bay off North Carolina was examined to determine the reliability of pigment patterns established from laboratory-reared material (Table 4). We examined the extent of pigment along the isthmus, lateral pigment in the caudal area, vomer and maxillary pigment, and the extent of pigment on the lateral surface of the gut of field-collected material. On the basis of our observations, caution must be used when relating pigmentation of laboratory-reared material to field-collected material. Generally, field-collected specimens had less intense pigmentation than those reared in the laboratory (Figs. 3–6). Our observations of vomer pigment, maxillary pigment, and lateral pigment on the surface of the gut on laboratory-reared larvae were not consistently observed on field-collected larvae (Table 4). Pigment on the lateral surface of the caudal area that aligned with the myosepta and ventral midline pigment that appeared to migrate dorsally on the lateral surface was observed only on *P. albigutta* larvae (laboratory-reared and field-collected). The presence of this pattern might aid in the separation of *P. albigutta* from *P. lethostigma*. However, the absence of this pattern has little value because field-collected *P. albigutta* may lack lateral caudal pigment (Table 4) and when present may not always be aligned with myosepta. On preflexion and flexion field-collected *Paralichthys* larvae, we were unable to define two distinct pigment types but were limited in the number of larvae available. Eight early preflexion larvae (approximately 2.6 mm NL) from Onslow Bay were examined for cranial spines, and only two spines or less were observed. We considered these to be *P. albigutta* on the basis of observations of laboratory-reared material. A collection of material that included early flexion larvae with three cranial spines would be useful 1) to verify the presence of three cranial spines in field-collected material and 2) to categorize larvae into two types (i.e. three cranial spines vs. ≤ two cranial spines) for a detailed examination of pigment patterns. In addition, the use of otolith characteristics produced during the early larval period may be useful in facilitating separation of *P. albigutta* and *P. lethostigma* (Laidig and Ralston, 1995).

Identification of field-collected specimens was based on stage of development of meristic characters (Gutherz, 1967) (Tables 1 and 2). Unless field-collected material is cleared and stained and then measured, the stage of development of meristic characters may not be a valid diagnostic character. The bodies of field-collected material generally are bent, and measurements taken before and after clearing and staining, which tend to straighten the bodies, may vary by 1 mm (Table 4). This is especially pertinent when attempting to identify flexion and early postflexion larvae by size at a developmental stage.

Two specimens of *Paralichthys squamilentus* postflexion larvae were tentatively identified from February collections in Onslow Bay. Pigment at the dorsal and ventral midline resembled *P. dentatus* (Fahay, 1983). One specimen (5.9 mm SL) had 10 postanal melanophores along the ventral midline. Lateral pigment in the caudal area was absent. The

Table 4

Selected field-collected specimens used to examine the effectiveness of pigmentation to identify gulf flounder, *Paralichthys albigutta*, and southern flounder, *P. lethostigma*, larvae. Species identification was determined by relating body length (measured on cleared and stained material) and ray formation. Presence of pigment indicated by a plus sign (+), absence by a minus sign (—).

Specimen number	Body length (mm) preserved	Body length (mm) cleared and stained	Caudal rays	Dorsal rays	Anal rays	Lateral gut pigment	Vomer pigment	Maxillary pigment	Pigment along entire length of isthmus	Lateral caudal pigment	Species identification
1	5.4 NL	6.2 NL	10	8	0	—	—	—	—	—	*P. albigutta*
2	5.2 NL	5.7 NL	8	5–6	0	—	—	—	—	—	*P. albigutta*
3	6.4 NL	7.3 SL	13	13–14	13	—	+	—	—	+	*P. lethostigma*
4	5.4 NL	6.0 SL	12	8	0	+	—	+	+	+	*P. albigutta*
5	5.6 NL	5.7 NL	11	6–7	0	+	+	+	+	+	*P. albigutta*
6	5.0 NL	5.2 NL	0	3	0	—	+	—	—	+	*P. albigutta*
7	5.5 NL	6.5 NL	10	8	0	—	—	—	—	+	Unknown
8	5.0 NL	5.7 NL	4	3	0	+	+	—	—	+	*P. albigutta*
9	5.4 NL	5.9 NL	6	3	0	—	—	—	—	—	*P. albigutta*
10	5.1 NL	5.7 NL	4–5	3	0	—	—	—	—	—	*P. albigutta*
11	7.8 SL	7.8 SL	17	68	41	—	—	—	—	—	*P. lethostigma*
12	6.7 SL	6.7 SL	17	10	0	—	—	—	—	—	*P. lethostigma*

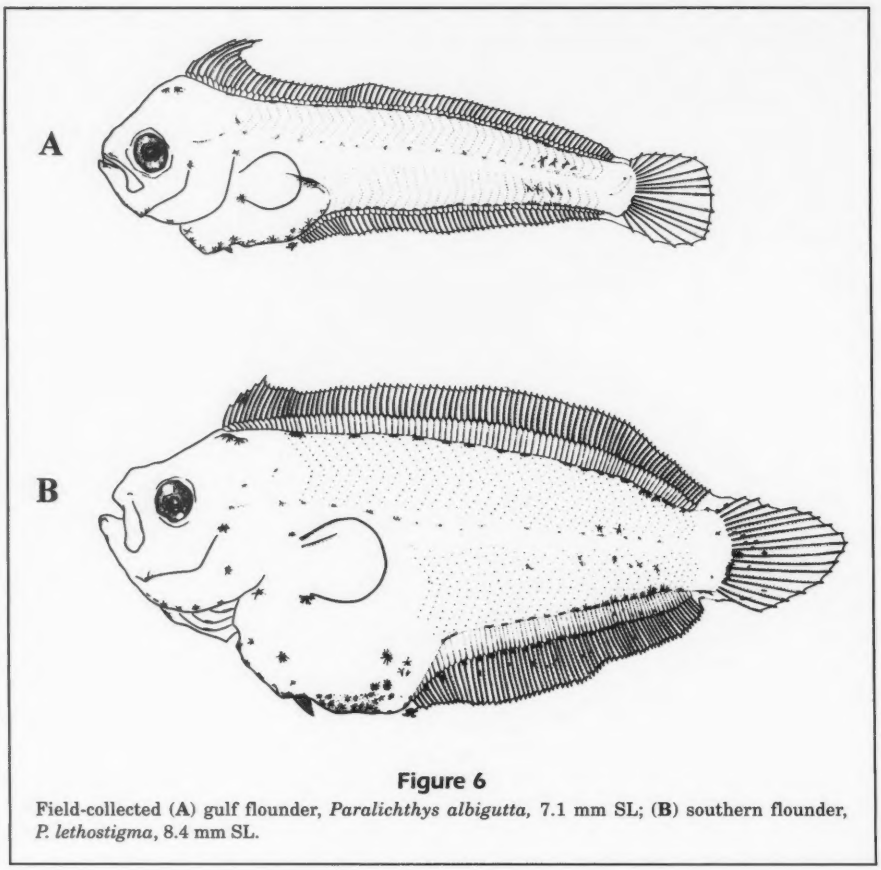

Figure 6

Field-collected (**A**) gulf flounder, *Paralichthys albigutta*, 7.1 mm SL; (**B**) southern flounder, *P. lethostigma*, 8.4 mm SL.

other specimen (6.2 mm SL), had 12 postanal melanophores along the ventral midline. One melanophore occurred on the lateral portion of the caudal area. We considered these specimens to be *P. squamilentus* because they were well developed for their size compared with *P. dentatus* (Fahay, 1983). Approximately 64 dorsal rays and 55 anal rays were formed. Neither the dorsal nor anal fins were completely formed. One specimen had four well-defined cranial spines and five preopercle spines. The other specimen had three cranial spines and five preopercle spines. Both specimens had 40 vertebrae.

Discussion

Paralichthys larvae can be separated from other bothid larvae by ventral midline pigment and the caudal formula when the principal caudal rays are formed (Fahay, 1983). *Paralichthys dentatus* and, tentatively, *P. squamilentus* larvae can be separated from *P. albigutta* and *P. lethostigma* larvae by differences in postanal ventral midline pigment (Fig. 7) and in size at development. *Paralichthys dentatus* has a maximum of 13 postanal melanophores along the ventral midline that are not uniform in size or spacing (Smith and Fahay, 1970). Tentatively, *P. squamilentus* has ventral midline pigment similar to *P. dentatus*. *Paralichthys albigutta* and *P. lethostigma* have approximately 19–31 postanal ventral midline melanophores that are uniform in size and spacing (Fig. 7). Larval *P. dentatus* can tentatively be separated from larval *P. squamilentus* by differences in development. At any given size, *P. squamilentus* appears to be significantly more developed than the other three *Paralichthys* species. However, early preflexion larvae might be difficult to separate from *P. dentatus* because *P. squamilentus* has only been tentatively described from two postflexion specimens (this study). On the other hand, at any given

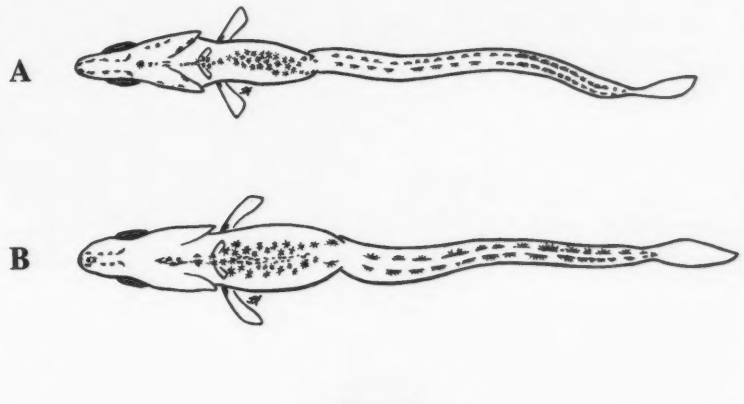

Figure 7

Pigmentation on the ventral side of field-collected, postflexion (**A**) gulf flounder, *Paralichthys albigutta* (9.1 mm SL), and (**B**) summer flounder, *P. dentatus* (9.7 mm SL).

size *P. dentatus* is the least developed of the four paralichthids (Fahay, 1983).

The best diagnostic character for separating *P. albigutta* from *P. lethostigma* is the development of meristic characters, but field-caught specimens must be cleared and stained prior to identification. At any given size, *P. albigutta* is more developed than *P. lethostigma* (Tables 1 and 2). The number of cranial spines could be useful in separating preflexion *P. albigutta* (zero to two spines) from preflexion *P. lethostigma* (three spines) if field-collected specimens are in concordance with those reared in the laboratory. Pigmentation on the lateral surface of the hindgut and caudal area are more developed in *P. albigutta* compared with *P. lethostigma*, but these characters may not be as consistent on wild specimens (e.g. Table 6). Caution should be used when extrapolating pigment patterns on laboratory-reared material to field-collected materials.

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Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *C. stigmaeus* within areas of upwelling off central California

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Abstract.—Upwelling and its associated offshore advection of surface waters can affect the recruitment of nearshore organisms. Late-stage pelagic Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, were collected with a midwater trawl off central California during the spring and summer upwelling season. In both species, otolith size increased linearly with metamorphic development; standard length, however, increased asymptotically. Earlier stages of both species occurred shallower in the water column, whereas later stages occurred deeper. The deeper distribution of later stages may have been due to decreased buoyancy as a result of increased otolith size and ossification of bony structures coincident with metamorphosis. Earlier stages of both species were more abundant offshore and less abundant in areas of upwelling, whereas later stages were more abundant nearshore regardless of upwelling. The difference in the horizontal distributions of early and late stages may have been passively driven by different current patterns as a result of the difference in vertical distributions between early and late stages.

Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, are abundant along the Pacific coast of North America (Miller and Lea, 1976). In both species, spawning peaks during the summer months but also occurs at lower levels during the remainder of the year; individuals may spawn more than once during a given season (Arora, 1951; Ford, 1965; Goldberg and Pham, 1987; Matarese et al., 1989; Rackowski and Pikitch, 1989). Sanddabs have a long pelagic stage, which may exceed 324 days in speckled sanddabs and 271 days in Pacific sanddabs (Kendall, 1992; Brothers[1]), and settle at a relatively large size (20 to greater than 39 mm standard length (SL) for Pacific sanddabs and 24 to greater than 36 mm for speckled sanddabs) (Ahlstrom et al., 1984; Matarese et al., 1989). Kramer (1990) noted that flatfish with nearshore nurseries had brief pelagic stages and settled at small sizes, whereas those with less restricted coastal nurseries had longer pelagic stages and settled at larger sizes. Kramer (1990) placed sanddabs in the latter category; however, speckled sanddabs, in particular, have a somewhat restricted bathymetric distribution as settled individuals (usually found at depths of 40 m and less)(Rackowski and Pikitch, 1989; Kramer, 1990). Both species are widely distributed as pelagic larvae (as far as 724 km offshore for Pacific sanddabs and 320 km offshore for speckled sanddabs) (Rackowski and Pikitch, 1989), but settled individuals occur within a somewhat more restricted coastal region.

The existence of late-stage Pacific and speckled sanddabs in midwater trawls conducted off central California by the National Marine Fisheries Service (NMFS) Tiburon Laboratory (Wyllie-Echeverria et al., 1990) provided an opportunity to examine ontogenetic changes in distribution associated with metamorphosis and settlement of these two sanddabs. In this paper we investigated the vertical and horizontal distribution of pelagic-stage sanddabs, with the general purpose of elucidating the changes that take place at metamorphosis and settlement. Because the NMFS collections were made during the spring

[1] Brothers, E. B. EFS Consultants, Ithaca, NY 14850. Personal commun., 1993.

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and summer upwelling season, when the associated offshore advection of surface waters can adversely affect marine organisms with pelagic life stages (Parrish et al., 1981; Bailey and Francis, 1985; Roughgarden et al., 1988), the effect of upwelling on pelagic-stage sanddabs was also investigated.

Methods

Data collection

Pelagic Pacific and speckled sanddabs were collected in conjunction with the annual juvenile rockfish surveys conducted by NMFS Tiburon Laboratory scientists aboard the National Oceanic and Atmospheric Administration (NOAA) research vessel *David Starr Jordan*. Standard stations extending from Point Reyes to Cypress Point (Fig. 1) were sampled with a 26 × 26 m modified Stauffer midwater trawl with a codend liner of 9.5-mm stretched mesh (Wyllie Echeverria et al., 1990). Standard trawling depth was 30 m except at shallow-water stations where trawls were conducted at 10 m. At certain standard stations a series of three depth-stratified trawls (depths=10 m, 30 m, and 110 m) were conducted to determine bathymetric distributional patterns (Fig. 1). As time permitted, additional trawls, both standard depth and depth-stratified, were conducted at nonstandard stations. All trawls were 15 minutes in duration and were completed between the hours of 2100 and 0600. Stations were sampled during a 10-day "sweep" of the survey area. Three replicate sweeps were completed from mid-May to mid-June of each year; in some years one additional sweep was completed in early April.

CTD (conductivity, temperature, and depth) casts were made at each trawl station to obtain temperature and salinity information at depth. Additional CTD casts were made during the day along tracklines interspersed between the trawl station lines (Schwing et al., 1990). Surface temperature and salinity were also recorded continuously by a thermosalinometer aboard the vessel. CTD and thermosalinometer data were used to determine the relation between upwelling and the spatial distributions of the different pelagic stages of both sanddabs.

Although the annual juvenile rockfish surveys began in 1983, sanddabs were not identified to species before 1987. Therefore, data were analyzed only from the 1987 through 1991 surveys. In addition to the May–June surveys in each year, sampling was carried out in April of 1987, 1988, and 1990. Sanddabs were identified and enumerated on board the research vessel at sea. In 1990 and 1991, samples were frozen after identification and enumeration and brought back to the laboratory where standard length (SL) and stage of metamorphosis were additionally recorded for each specimen collected. Five metamorphic stages, based on the staging system used by Pearcy et al. (1977), were defined as follows:

Stage 1 = left and right eyes positioned symmetrically on both sides of head;
Stage 2 = right eye has begun to move dorsally;
Stage 3 = upper edge of right eye within close proximity to the top of the right side of the head;
Stage 4 = right eye has begun to cross over to the left side of the head;
Stage 5 = right eye completely crossed over to left side of the head.

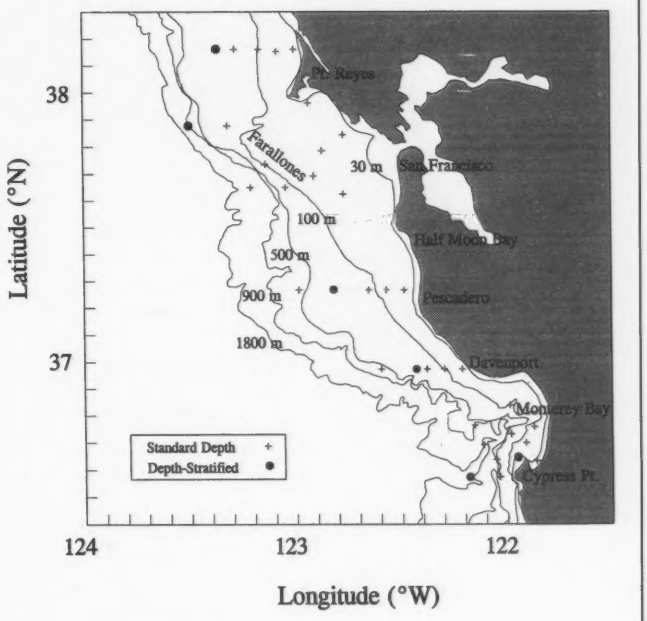

Figure 1
Location of standard trawling stations for Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected during 1987–91.

No stage-1 individuals were collected, probably because their small size allowed them to pass through the net.

To determine if metamorphic stage was a more useful character than SL in resolving spatial patterns, twenty individuals from each metamorphic stage of each species were randomly selected from the May to June survey of 1991, and their otoliths were removed. The diameter of the largest otolith, the sagitta, was measured with a compound microscope connected to a video camera, monitor, digitizer, and computer.

Data analysis

Statistical analyses were performed by using the program SAS (SAS Institute, Inc., 1988). Abundances were transformed by $\ln(x+1)$ to normalize the data. Mean abundances from the April surveys and for each sweep of the May–June surveys were then calculated for all standard stations successfully sampled to describe temporal differences in abundance.

Means and ranges of SL's of the metamorphic stages of both sanddab species were calculated by using specimens measured from the April and May–June surveys of 1990 and from the May–June survey of 1991. Mean SL's were calculated separately for the specimens randomly selected for otolith removal in order to compare the observed changes in otolith size relative to metamorphic stage with SL. Tukey's studentized range tests were performed to determine if there were significant differences in SL and otolith diameter with metamorphic development.

Owing to changes in the width of the net mouth with depth (width=8 m at 10 m depth, 11 m at 30 m depth, and 13.5 m at 110 m depth), abundances for the depth-stratified trawls were adjusted prior to analysis (Lenarz et al., 1991). Abundances for 10-m depth trawls were multiplied by 11/8, abundances for 30-m depth trawls were not adjusted, and abundances for 110-m depth trawls were multiplied by 11/13.5. Because of the large spatial variability in abundances and the fact that not all depth-stratified trawls sampled every depth (i.e. because of time constraints only the 10 m and 30 m depths were sampled at some stations, and only the 30 m and 110 m depths were sampled at others), differences in abundance with depth were evaluated by paired comparison *t*-tests. Pairing was by station; each depth pair available was considered (10 m versus 30 m, 30 m versus 110 m, and 10 m versus 110 m). When both observations of a pair were equal to 0, that pair was deleted from the analysis. To determine if there was a seasonal change in depth distribution, analyses were performed on all the surveys from 1987 to 1991, the April surveys alone, and the May–June surveys alone. To determine changes in vertical distribution with development, the paired comparisons were also carried out on each of the metamorphic stages, by using data from the April and May–June surveys of 1990 and from the May–June survey of 1991.

To determine the similarity of horizontal distributions among metamorphic stages, Spearman rank correlation coefficients were calculated for the abundances of different stages over standard stations during the 1990 and 1991 surveys.

CTD salinity at the surface (average salinity at 3–5 m depth) and at the standard mid-depth of 30 m (average salinity at 28–32 m) from each sweep of the May–June surveys of 1990 and 1991 was contoured by using the Kriging option in the program SURFER (Golden Software, Inc., 1990). Owing to problems with the CTD during the second sweep of the May–June survey of 1991, thermosalinometer data were incorporated into the available CTD data to generate the surface contours. The log-transformed abundances of metamorphic stages 2 and 5 were overlaid onto the salinity contours to observe the relation (if any) between the abundances of these two metamorphic stages and salinity features indicative of coastal upwelling. These two stages had the greatest potential for differences in spatial relations with salinity features, given that stage-2 individuals were not competent for settlement, whereas stage-5 individuals were relatively close to settlement.

Thermosalinometer data were used to determine trawls conducted in areas of recent upwelling. Schwing et al. (1991) designated recently upwelled water as having surface temperatures less than 10.5°C and surface salinities greater than 33.6 ppt. We used surface salinities greater than 33.6 ppt but surface temperatures less than 11.0°C to allow for marginal surface layer warming during the daylight hours prior to the nighttime trawls. Log-transformed abundances obtained at standard stations from the May–June surveys of 1990 and 1991 were converted to standard scores (log-transformed abundances rescaled for each year so that mean=0 and standard deviation=1) to adjust for year effects, allowing the data from both years to be combined. *T*-tests were used to compare the mean standard scores of metamorphic stages in upwelling and non-upwelling areas. Separate analyses were performed for shallow-depth (10-m) trawls and standard mid-depth (30-m) trawls because of the possibility of a depth effect due to metamorphic stage and the fact that upwelling typically affects only the upper 20 m of the water column (Parrish et al., 1981). To increase sample size, trawls at nonstandard stations were included in the analysis.

Results

Overall abundances and seasonal abundance patterns of the two sanddab species were variable (Fig. 2). In 1991, the abundance of both species increased monotonically during the May–June sampling period, whereas in 1987 and 1988, catches were relatively high in April but showed a marked decrease by the end of May–June, suggesting that pelagic sanddab abundance frequently declines during the April–June period (Fig. 2). However, catches of Pacific sanddabs in April of 1990 were low relative to May–June, and the May–June catches in 1988 and 1989 did not change monotonically, suggesting interannual variation in seasonal patterns (Fig. 2). Although April–June abundances were variable (Fig. 2), the interannual variation in year-class strength of pelagic sanddabs could not be determined without complete seasonal data.

In both species, SL increased asymptotically with metamorphic stage (Fig. 3). In addition, the range of lengths within each stage was quite large (Fig. 3). Pacific sanddabs were generally larger than speckled sanddabs at each metamorphic stage (Fig. 3). Although stage-2 individuals were significantly smaller than individuals of subsequent stages, the mean SL's did not differ significantly among the three later stages (α=0.05, df=76 for Pacific sanddabs and df=75 for speckled sanddabs). Whereas SL increased asymptotically with metamorphic development in both sanddabs, otolith diameter showed a linear increase (Fig. 4). In addition, otolith diameter increased dramatically with SL (Fig. 5), and mean otolith diameter increased significantly with each successive stage (α=0.05, df=76 for Pacific sanddabs and df=75 for speckled sanddabs). It appears that metamorphosis in sanddabs is possible at a range of sizes (30 mm to >50 mm SL in Pacific sanddabs and 25 to 40 mm SL in speckled sanddabs) and that once initiated, there is little growth in length but continued otolith growth (Figs. 3–5).

In general, Pacific sanddabs were relatively evenly distributed throughout the water column; there was a slight decrease in abundance with increasing depth (Table 1). Separate analyses of the April and May–June surveys showed similar results (Table 1).

In contrast to Pacific sanddabs, speckled sanddabs were significantly more abundant in shallow and mid-depth trawls than in deep trawls (Table 2). Analyzed separately, the May–June surveys showed a similar pattern to the overall analysis, but the April surveys showed less distinct differences in depth distribution (Table 2). The April surveys showed a trend of decreased abundance in deep trawls relative to shallow and mid-depth trawls, but the differences were not significant (Table 2).

Depth distributions differed among the metamorphic stages of both sanddab species. Stage-2 individuals of Pacific sanddabs were significantly more abundant in mid-depth trawls than in deep trawls, with a trend for increased abundance in shallow trawls versus deep trawls (Table 3; Fig. 6). Although both stage-3 and stage-4 sanddabs showed a relatively even distribution throughout the water column (with no significant differences among depths), stage-3 individuals tended to be less abundant with increased depth, whereas stage-4 individuals tended to be more abundant with increased depth (Table 3; Fig. 6). Stage-5 individuals were generally less abundant in shallow trawls and showed a tendency toward increased abundance with increased depth (Table 3; Fig. 6).

In speckled sanddabs, stage-2 individuals were significantly more abundant in mid-depth trawls

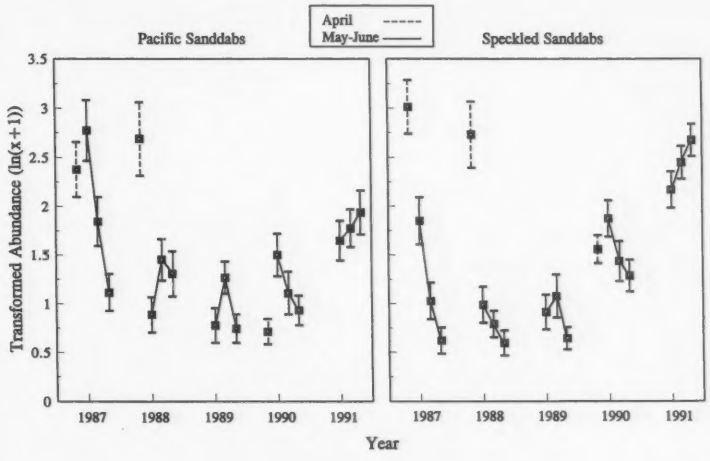

Figure 2

Means and standard errors of the log-transformed abundances of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected at standard stations during April and May–June 1987–91 (means of the three sweeps for the May–June surveys are connected by a line).

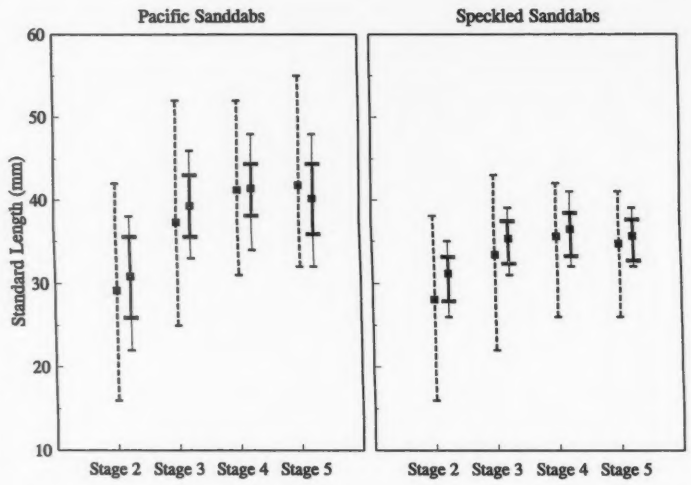

Figure 3

Means and ranges of standard lengths of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, in 1990 and 1991 as a function of metamorphic stage. All specimens measured are represented by dotted lines; those subsampled for otolith removal are represented by solid lines. Standard deviations for the specimens selected for otolith removal are shown with thick lines; ranges are shown with thin lines.

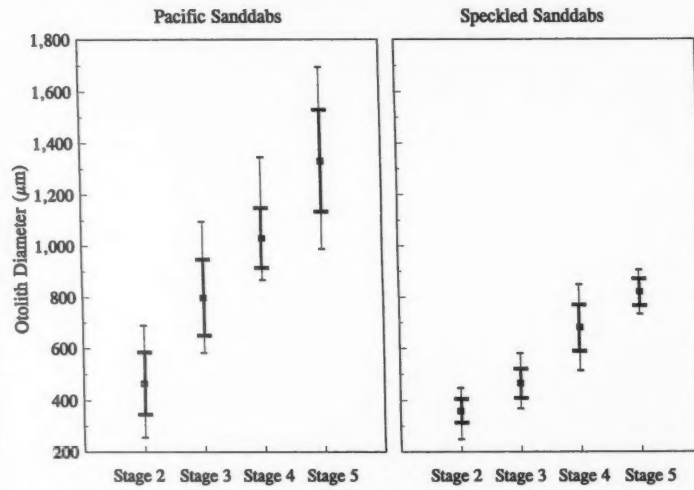

Figure 4

Means, standard deviations, and ranges of otolith diameters of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991. Standard deviations are shown with thick lines; ranges are shown with thin lines.

Table 1

Paired comparison *t*-tests of log-transformed abundance (ln(*x*+1)) of Pacific sanddabs, *Citharichthys sordidus*, from 1987 to 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
All surveys					
10 m – 30 m	57	0.07	0.1723	0.4047	0.6872
30 m – 110 m	63	0.03	0.1358	0.2075	0.8363
10 m – 110 m	39	0.43	0.2122	2.0419	0.0482
April surveys					
10 m – 30 m	15	0.11	0.4375	0.2515	0.8051
30 m – 110 m	11	–0.35	0.3193	–1.0889	0.3018
10 m – 110 m	8	0.53	0.5727	0.9192	0.3886
May–June surveys					
10 m – 30 m	42	0.06	0.1779	0.3109	0.7574
30 m – 110 m	52	0.11	0.1491	0.7223	0.4734
10 m – 110 m	31	0.41	0.2278	1.7962	0.0825

Table 2

Paired comparison *t*-tests of log-transformed abundance (ln(*x*+1)) of speckled sanddabs, *Citharichthys stigmaeus*, from 1987 to 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
All surveys					
10 m – 30 m	54	–0.01	0.1379	–0.1024	0.9188
30 m – 110 m	51	0.62	0.1395	4.4494	0.0001
10 m – 110 m	37	0.69	0.1555	4.4301	0.0001
April surveys					
10 m – 30 m	14	0.02	0.3319	0.0499	0.9610
30 m – 110 m	13	0.59	0.3488	1.7036	0.1142
10 m – 110 m	8	0.75	0.3479	2.1487	0.0687
May–June surveys					
10 m – 30 m	40	–0.02	0.1484	–0.1675	0.8678
30 m – 110 m	38	0.63	0.1476	4.2666	0.0001
10 m – 110 m	29	0.67	0.1768	3.8038	0.0001

than in deep trawls with a trend for increased abundance in shallow trawls versus deep trawls (Table 4; Fig. 6). Stage-3 and stage-4 individuals were most abundant in mid-depth trawls; stage-3 individuals showed a tendency for decreased abundance in shallow trawls versus mid-depth trawls (Table 4; Fig. 6). Stage-5 individuals were distributed relatively evenly throughout the water column, with a tendency toward increased abundance with increased depth (Table 4; Fig. 6). In contrast to Pacific sanddabs, of the four metamorphic stages, only stage-5 individuals of speckled sanddabs were abundant in the deep trawls (Table 4; Fig. 6). Thus, speckled sanddabs generally occurred shallower in the water column than did Pacific sanddabs (Fig. 6).

Within each species of sanddab, abundances of adjacent metamorphic stages were correlated over stations (Table 5). However, the correlations decreased among more dissimilar stages, indicating changes in distribution with advancing metamorphosis (Table 5). The only two stages in either species that were not significantly correlated with each other were stages 2 and 5 (Table 5). Results of the correlation analysis provided a substantial basis for overlaying only stage-2 and stage-5 abundances onto the salinity contours in Figures 8 and 9.

CTD salinity contours showed that many of the patterns at the surface were still noticeable at 30 m (Fig. 7; and Sakuma, 1992). Therefore, only the surface salinity contours were used because they provided the widest horizontal spatial coverage (salinity at 30 m was not available for nearshore stations because of the shallow bottom depth).

Table 3

Paired comparison *t*-tests of log-transformed abundance (ln(*x*+1)) of each metamorphic stage of Pacific sanddabs, *Citharichthys sordidus*, from 1990 and 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	*n*	Mean diff.	SE	*t*	*P*
Stage 2					
10 m – 30 m	16	0.08	0.3686	0.2217	0.8276
30 m – 110 m	15	0.53	0.2073	2.5674	0.0224
10 m – 110 m	14	0.65	0.3890	1.6758	0.1176
Stage 3					
10 m – 30 m	14	0.09	0.4787	0.1846	0.8564
30 m – 110 m	17	0.25	0.2058	1.2234	0.2389
10 m – 110 m	16	0.34	0.3987	0.8649	0.4007
Stage 4					
10 m – 30 m	10	–0.55	0.4237	–1.3017	0.2254
30 m – 110 m	12	–0.05	0.3156	–0.1684	0.8693
10 m – 110 m	13	–0.51	0.3946	–1.2940	0.2247
Stage 5					
10 m – 30 m	15	–0.77	0.3505	–2.1952	0.0455
30 m – 110 m	16	–0.35	0.2927	–1.1901	0.2525
10 m – 110 m	13	–0.70	0.3931	–1.7859	0.0994

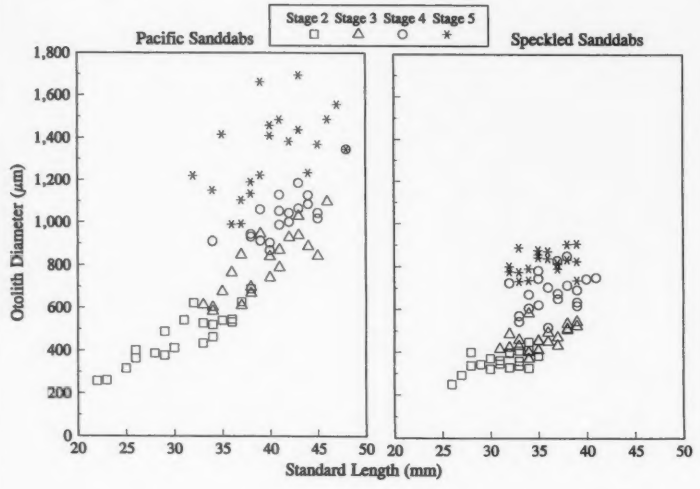

Figure 5

Otolith diameter versus standard length of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991.

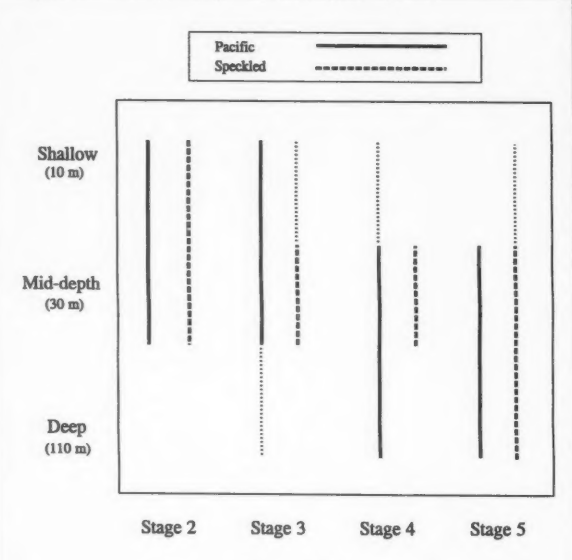

Figure 6

Depth distributions of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in 1990 and 1991, based on paired comparisons of abundance at different depths (Tables 3 and 4). Small dotted lines indicate nonsignificant ($P>0.05$) trends of decreased abundance at the given depth.

Contours for sweep 1 of the May–June survey of 1990 showed a pattern of recent or ongoing upwelling occurring off Point Reyes and the Davenport area (see Fig. 1 for place names) as evidenced by the filaments of higher salinity water projecting seaward and shoreward impingement of lower salinity, more oceanic water (Simpson, 1987) at the surface north of Point Reyes (Fig. 8). The contours for sweep 2 indicated a reduction in offshore transport due to upwelling, with lower salinities closer to shore (Fig. 8). The contours for sweep 3 showed upwelling activity occurring off Point Reyes but not off Davenport (Fig. 8).

The contours for the May–June survey of 1991 showed pronounced seaward filaments off Point Reyes and Davenport during sweep 1, which indicated recent or ongoing upwelling (Fig. 9). During sweep 2, upwelling was still evident off Davenport, but owing to problems with the CTD, patterns off Point Reyes were not easily discernible (Fig. 9). During sweep 3, there was a relaxation of upwelling as evidenced by the lack of seaward-projecting filaments of higher salinity water (Fig. 9).

The overlaid abundances of stages 2 and 5 showed that large abundances of stage-5 individuals of both species generally occurred nearshore and could be found within centers of upwelling (Figs. 8 and 9 off Davenport and Monterey Bay; Fig. 9 off Point Reyes). In contrast, large numbers of stage-2 individuals of both species were relatively more abundant in the offshore transitional zone between coastal water (nearshore, high salinity due to upwelling) and oceanic water (offshore, low salinity) (Figs. 8 and 9). In addition, large numbers of stage-2 individuals were observed nearshore in the area north of Point Reyes during sweep 1 of 1990 associated with the shoreward impingement of oceanic water (Fig. 8).

Although the effects of upwelling would be expected to be most intense near the surface, no significant differences in the abundances of the metamorphic stages of either sanddab species were observed between upwelling and nonupwelling areas at the shallow trawl depth of

Table 4

Paired comparison *t*-tests of log-transformed abundance (ln(x+1)) of each metamorphic stage of speckled sanddabs, *Citharichthys stigmaeus*, from 1990 and 1991 at depth-stratified stations. If both numbers within a pair were = 0, that pair was deleted from the analysis.

Depth pair	n	Mean diff.	SE	t	P
Stage 2					
10m – 30 m	21	–0.08	0.2339	–0.3240	0.7493
30m – 110 m	18	0.49	0.2408	2.0436	0.0568
10m – 110 m	14	0.52	0.3199	1.6392	0.1251
Stage 3					
10m – 30 m	23	–0.46	0.2438	–1.8982	0.0709
30m – 110 m	17	0.51	0.2350	2.1629	0.0460
10m – 110 m	16	0.44	0.2647	1.6492	0.1199
Stage 4					
10m – 30 m	17	–0.79	0.2212	–3.5700	0.0026
30m – 110 m	14	0.67	0.2532	2.6485	0.0201
10m – 110 m	10	0.05	0.2604	0.1739	0.8658
Stage 5					
10m – 30 m	10	–0.72	0.4615	–1.5548	0.1544
30m – 110 m	4	–0.27	0.3705	–0.7186	0.5243
10m – 110 m	5	0.11	0.4416	0.2584	0.8088

Table 5

Spearman rank correlations of log-transformed abundance (ln(x+1) of each metamorphic stage of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected at standard stations during 1990 and 1991 (significance probabilities of each correlation are listed in bold type under the coefficients).

	Pacific sanddabs (n = 257)			
	Stage 2	Stage 3	Stage 4	Stage 5
Stage 2		0.58	0.31	0.06
		0.0001	**0.0001**	**0.3559**
Stage 3	0.62		0.47	0.13
	0.0001		**0.0001**	**0.0316**
Stage 4	0.15	0.37		0.38
	0.0181	**0.0001**		**0.0001**
Stage 5	0.04	0.13	0.53	
	0.4827	**0.0346**	**0.0001**	
	Stage 2	Stage 3	Stage 4	Stage 5
	Speckled sanddabs (n = 257)			

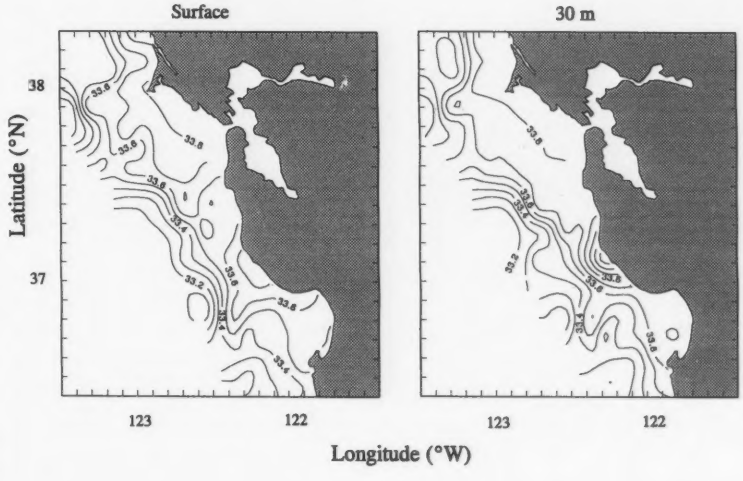

Figure 7

Salinity contours at the surface compared with salinity contours at 30 m depth during 1990 sweep 1.

10 m (Table 6; Fig. 10). However, at the mid-depth of 30 m, stages 2 and 3 of Pacific sanddabs were significantly less abundant in upwelling areas than in non-upwelling areas, and stages 2 and 3 of speckled sanddabs showed a strong tendency for decreased abundance in upwelling areas (Table 6; Fig. 10). In contrast, stage 5 in each species tended to be more abundant in upwelling areas than in non-upwelling areas (Table 6; Fig. 10).

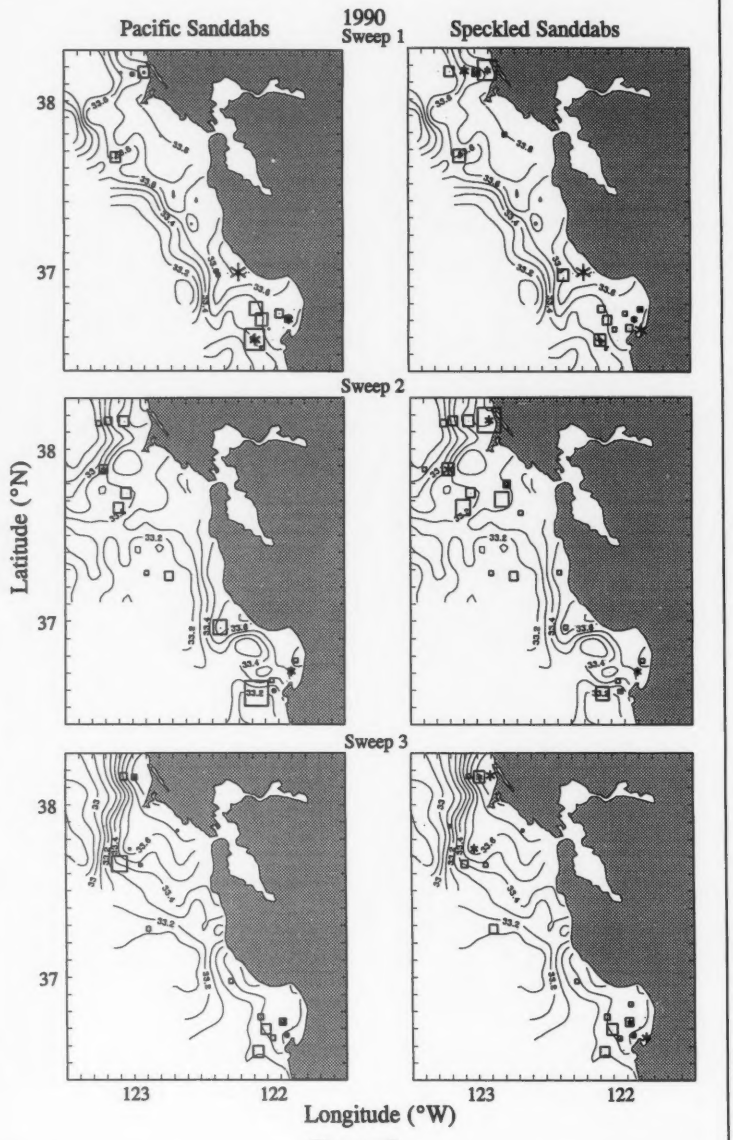

Figure 8

Salinity contours at the surface during the May–June survey of 1990 with overlaid abundances of stages 2 (represented by squares) and 5 (represented by asterisks) of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*. Size of each symbol is proportional to the abundance.

Discussion

During the springtime series covered by this study, metamorphosis in both sanddab species occurred at a wide range of sizes, indicating little growth in body size during metamorphosis (Figs. 3 and 5). Later metamorphic stages tended to occur in deeper water than did earlier stages; Pacific sanddabs shifted to deeper water at earlier stages than speckled sanddabs (Tables 3 and 4; Fig. 6). Later metamorphic stages of both sanddabs occurred nearer to shore than earlier stages, despite the upwelling-associated offshore advection of surface waters (Table 6; Figs. 8–10).

Given the reported variability of size at metamorphosis in both sanddab species (Ahlstrom et al., 1984; Matarese et al., 1989), it was not surprising to observe a large amount of overlap in the SL's of the different metamorphic stages (Fig. 3). Kendall (1992) reported that speckled sanddabs settled at ages ranging from 113 to 324 days. In general, she found that larger, recently settled individuals had spent more time in the plankton than smaller recently settled ones (Kendall, 1992). Kendall (1992) also reported that settlement marks on the otoliths of speckled sanddabs were generally observed at an otolith radius of 400–450 μm. This corresponds to the otolith diameters observed in stage-5 individuals, indicating that these individuals were prepared to settle (Figs. 4 and 5).

An important aspect of metamorphosis in flatfishes is the

ossification of bony structures (Ahlstrom et al., 1984). The large increase in otolith size observed in later metamorphic stages of both sanddab species may be attributable to the transition from a planktonic form to a benthic form. Jenkins (1987) observed accelerated otolith growth in relation to growth in length at the beginning of metamorphosis for the flatfish *Rhombosolea tapirina*, which resulted in significant alterations in otolith increment morphology. One alteration in otolith morphology observed in pelagic stage Pacific sanddabs was the formation of accessory growth primordia. Accessory growth primordia first occurred in stage-3 individuals and completely enclosed the otolith by stage 5 (Brothers[1]). Toole et al. (1993) found that the initiation of accessory primordia formation was coincident with the onset of eye migration in Dover sole, *Microstomus pacificus*, and that the completion of accessory primordia formation occurred either during the final stages of eye migration in pelagic individuals or shortly after settlement.

Metamorphosis in some flatfish can take place in as little as five hours, as in *Cynoglossus macrostomus* (Ahlstrom et al., 1984), or up to nine months, as in *Microstomus pacificus* (Markle et al., 1992). The small increase in length seen in metamorphosing sanddabs (Figs. 3 and 5) suggests a relatively rapid metamorphosis relative to growth. However, if metamorphosis occurred very rapidly, then the probability of collecting metamorphosing specimens would be small (Laroche et al., 1982; Ahlstrom et al., 1984). The large numbers of later stages collected in 1991 and the large otolith sizes in later stages suggest that metamorphosis in both sanddab species occurs over a more prolonged period of time (Figs. 5, 8, and 9). Preliminary results from Pacific sanddab otoliths indicate that the transition from stage 3 to stage 5 takes approximately three weeks (Brothers[1]). Kendall's (1992) data on otolith radius at age indicate that the transition from individuals with otolith radii correspond-

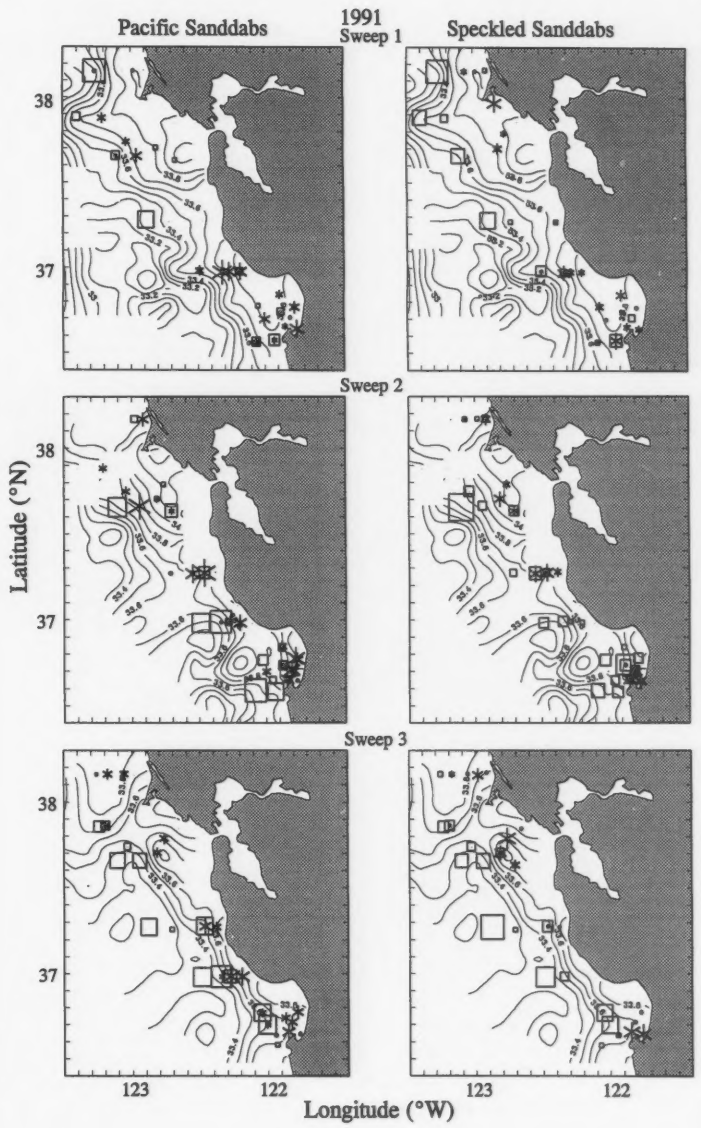

Figure 9

Salinity contours at the surface during the May–June survey of 1991 with overlaid abundances of stages 2 (represented by squares) and 5 (represented by asterisks) of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*. Size of each symbol is proportional to the abundance.

Table 6

Comparison of standard scores of log-transformed abundance (ln(x+1)) of each metamorphic stage of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, in upwelling and non-upwelling areas during 1990 and 1991 (upwelling areas were defined as having surface salinities >33.6 ppt and surface temperatures <11.0°C). Means and standard errors are shown in Figure 10. Degrees of freedom less than $(n_1-1)+(n_2-1)$ indicate cases with unequal variances.

Pacific sanddabs				Speckled sanddabs			
Stage	*t*	df	*P*	Stage	*t*	df	*P*
Shallow trawls (upwelling *n*=36, non-upwelling *n*=44)							
2	0.6797	78.0	0.4987	2	–0.4730	76.2	0.6375
3	0.6911	76.4	0.4916	3	0.6346	78.0	0.5275
4	0.1171	78.0	0.9071	4	0.4846	78.0	0.6293
5	–0.4135	77.0	0.6804	5	–0.3190	78.0	0.7506
Mid-depth trawls (upwelling *n*=63, non-upwelling *n*=99)							
2	–2.3877	159.9	0.0181	2	–1.7268	160.0	0.0861
3	–3.0253	160.0	0.0029	3	–1.7147	160.0	0.0883
4	–0.5325	160.0	0.5951	4	0.7201	160.0	0.4275
5	0.9655	160.0	0.3259	5	1.5650	100.4	0.1207

ing to stage 3 to those corresponding to stage 5 takes approximately five weeks.

Morphological changes associated with metamorphosis probably decrease the buoyancy of pelagic sanddabs. Laroche et al. (1982) found an increase in otolith growth relative to growth in length at metamorphosis for *Parophrys vetulus*, which was similar to that observed for the two sanddab species in this study and for *Rhombosolea tapirina* (Jenkins, 1987). Reared *Parophrys vetulus* that were close to settlement frequently rested on their sides on the bottom and swam with their bodies at an angle (Laroche et al., 1982). This behavior may be related to decreased buoyancy as a result of the ossification of bony structures and to the large increase in otolith size (Laroche et al., 1982). In addition, the gas bladder is lost during metamorphosis in some species of flatfish, including the related Atlantic species *Citharichthys arctifrons* (Richardson and Joseph, 1973; Ahlstrom et al., 1984). Laidig[2] observed that the gas bladder was reduced in stage-4 Pacific sanddabs and absent in 90% of stage-5 specimens.

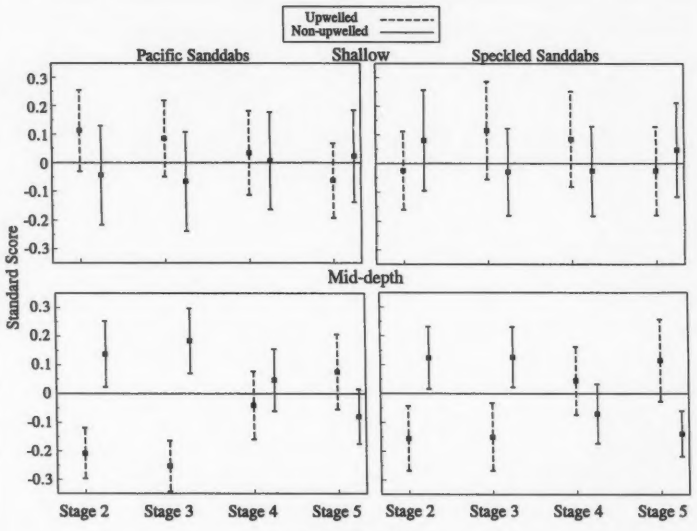

Figure 10

Mean standard scores and standard errors of metamorphic stages of Pacific and speckled sanddabs, *Citharichthys sordidus* and *C. stigmaeus*, collected in shallow and mid-depth trawls during 1990 and 1991 in upwelling and non-upwelling areas (upwelling=surface salinity >33.6 ppt and surface temperature <11°C).

[2] Laidig, T. E. Tiburon Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Drive, Tiburon, CA 94920. Personal commun., 1994.

The decrease in buoyancy due to increased otolith size, the ossification of other bony structures, and the loss of the gas bladder may account for the deeper bathymetric distribution of later metamorphic stages in both sanddab species (Tables 3 and 4; Fig. 6). The greater water density at deeper depths may reduce the energy expenditure required for less buoyant fish to remain pelagic; however, beyond a given range of SL and otolith size, individuals may sink more rapidly. Therefore, the decrease in buoyancy may account directly for the deeper bathymetric distribution of later-stage pelagic sanddabs, although fish may behaviorally seek deeper water as well.

Lenarz et al. (1991) reported that younger, smaller juveniles of the shortbelly rockfish, *Sebastes jordani,* were found deeper in the water column than larger individuals during May–June. It was suggested that the smaller individuals were adapted to seeking deeper water as a method of avoiding offshore advection due to upwelling (Lenarz et al., 1991). In contrast, the early stages of both sanddab species showed a shallower distribution than the later stages (Tables 3 and 4; Fig. 6). The shallow distribution of early stages may explain the comparisons of abundance in upwelling and non-upwelling areas for the 30-m depth trawls, which suggest that early stages are subject to offshore advection due to coastal upwelling (Table 6; Figs. 6, 8, 9, and 10). The offshore advection of early stages may also explain their predominantly offshore distribution (Figs. 8 and 9).

The lack of significant differences in abundance between upwelling and non-upwelling areas for the shallow depth trawls observed in both sanddab species might be explained by the fact that the majority of these trawls were conducted nearshore where early stages were generally less abundant and that later stages were generally less abundant at the shallow trawl depth (Tables 3, 4, and 6; Figs. 6, 8, 9, and 10). In contrast, the 30-m mid-depth trawls, in which most metamorphic stages occurred, were more widely distributed and probably indicated better the relation between upwelling and the distribution of metamorphic stages (Tables 3, 4, and 6; Fig. 6). Figure 10 shows a change in distribution of metamorphic stages in the 30-m mid-depth trawls; earlier stages tended to be more abundant in water that had not been upwelled recently, whereas later stages were more abundant in recently upwelled water.

The reduction in abundance of early stages in trawls within upwelling areas may have been due to the fact that these stages were present predominantly offshore while upwelling events occurred nearshore (Figs. 8 and 9). However, the large abundances of stage-2 individuals of both species observed nearshore north of Point Reyes during sweep 1 of 1990 associated with an extension of oceanic waters toward shore (Fig. 8) and the large abundances of stage-2 individuals occurring within the transitional areas between offshore oceanic waters and nearshore coastal waters (Figs. 8 and 9) suggest that these early stages were subject to transport by ocean currents. Analysis of California Cooperative Oceanic Fisheries Investigations (CalCOFI) data by Ahlstrom and Moser (1975) and Loeb et al. (1983) indicated that the larvae of both sanddab species were collected both nearshore and well offshore. Therefore, sanddabs of both species are probably passive drifters during their early life history stages as evidenced by the predominantly offshore distribution of their early metamorphic stages (Figs. 8 and 9) and the somewhat dispersed distribution of their larvae (Ahlstrom and Moser, 1975; Loeb et al., 1983).

In contrast to the distributional patterns of early stage metamorphic sanddabs, the tendency for later stages of both species to be more abundant in upwelling areas was probably due to the fact that later stage individuals occurred predominantly nearshore (Figs. 8 and 9). Although large numbers of stage-5 individuals of both species occurred within upwelling plumes (Figs. 8 and 9), large abundances of stage-5 individuals could also be found nearshore in areas outside of the upwelling plumes (Figs. 8 and 9). Because later-stage individuals were more abundant at deeper depths, they were probably less susceptible to offshore advection by upwelling. The deeper and more shoreward distribution of later-stage sanddabs parallels the observations of Barnett et al. (1984) on later stages of northern anchovy, *Engraulis mordax*, white croaker, *Genyonemus lineatus*, and queenfish, *Seriphus politus*, off southern California. Larson et al. (1994) also found that late-stage pelagic juvenile rockfish (*Sebastes* spp.) off central California had a more shoreward distribution, although there was no evidence that later-stage fish were distributed at greater depths (Lenarz et al., 1991).

In summary, it appears that physical changes in metamorphosing sanddabs are correlated with changes in their depth distributions; more developed, less buoyant individuals occur deeper in the water column (Fig. 6). This may influence the horizontal distributions of pelagic sanddabs in the upwelling regions off central California. Early-stage sanddabs present within the upper mixed layer would be subject to offshore advection associated with coastal upwelling or to onshore advection associated with downwelling (Table 6; Figs. 8–10). In contrast, the deeper distribution of later-stage sanddabs decreases their susceptibility to upwelling-associated offshore advection and could potentially lead to onshore advection facilitated by the shoreward movement of

deeper water (Tables 3 and 4; Fig. 6). In addition, the vertical and horizontal distributions of both early and late-stage sanddabs may have a substantial behavioral component; however, the means to resolve such behavioral patterns is beyond the scope of this study.

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Review of new world hagfishes of the genus *Myxine* (Agnatha, Myxinidae) with descriptions of nine new species

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Abstract.—Nine new species of hagfishes (Myxinidae, *Myxine*) from the Pacific and Atlantic coasts of North and South America are described and a key is offered to the new world hagfishes. New data are presented for *Myxine circifrons* from the eastern Pacific Ocean, *M. limosa* from the northwestern Atlantic Ocean, and *M. affinis* and *M. australis* from in and near the Straits of Magellan. *Myxine limosa* is removed from the synonymy of *M. glutinosa*. The nine new species occur as follows: *M. hubbsi* along the Pacific coast from San Francisco, California, to Valparaiso, Chile; *M. hubbsoides* and *M. pequenoi* near Valdivia, Chile; *M. mccoskeri* and *M. robinsi* in the southern portion of the Caribbean Sea; *M. fernholmi, M. knappi,* and *M. dorsum* near the Falkland Islands, and *M. debueni* in the Straits of Magellan. *Myxine mccoskeri* and *M. pequenoi* are regarded as dwarfed, containing nearly mature eggs or testes at total lengths of 230 and 175 mm, respectively. Hermaphroditism is often found in individuals of *M. hubbsi, M. limosa,* and *M. affinis*.

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Hagfishes (slime eels) are cartilaginous, eel-like, abundant bottom-dwelling scavengers occurring at depths ranging from a few to at least 2,400 meters. *Myxine* is one of the six recognized genera in the "agnathan" family Myxinidae (Nelson, 1994). In the new world it comprises eight species in the Atlantic Ocean and six in the Pacific (references in this study); species occurring in the Straits of Magellan also may occur in either ocean. The genus *Myxine,* which presently contains 19 species including those in this study, is characterized principally by all the efferent gill pouch ducts discharging into a single aperture on each side, the left being confluent with the pharyngocutaneous duct. This character is shared by the genera *Neomyxine* Richardson, 1953, and *Nemamyxine* Richardson, 1958. *Neomyxine* is further characterized by having paired lateral finfolds in the prebranchial region, as well as the usual ventral finfold posterior to the gill apertures. In *Nemamyxine,* the body is extremely slender and the ventral finfold extends far forward nearly to the anteriormost prebranchial slime pores. In all other myxinids the ventral finfold does not extend anterior to the pharyngocutaneous duct. Head grooves ("lateral lines" of earlier authors) are lacking in genus *Myxine* as are the external eyespots common in genus *Eptatretus* (McMillan and Wisner, 1984). Hermaphroditism does not occur in our material of *M. circifrons* but is not uncommon in *M. limosa, M. affinis, M. australis, and M. hubbsi* and occurs in two of the three specimens of *M. hubbsoides.* The remaining new species have too few specimens to state with certainty whether or not hermaphroditism occurs among them. Great variation in developmental stages of eggs occurs among specimens of the same length and possibly age, which supports a widely held belief that hagfishes spawn throughout the year. As eggs mature, the polar caps enlarge into dome-like structures containing anchor filaments that are connected to the eggs when they are extruded. With one exception (a female *M. limosa* discussed below), eggs of all specimens examined here were not fully mature; polar caps were not visible, nor were they still encapsulated.

This study of new world hagfishes, the latest by us in a series on the family Myxinidae begun by Carl L. Hubbs (deceased), includes all 14 known species of *Myxine* from the Pacific and Atlantic coasts of North and South America. We have added old world *M. glutinosa* to all tables for comparison with the closely related *M. limosa.* Of the other four

known species, *M. ios* from the eastern Atlantic and *M. capensis* from South Africa are compared briefly with the new world species *M. pequenoi.* Both *M. garmani,* and *M. paucidens* Regan, 1913 are known only from Japan and are not closely related to any new world species. The number of new species (nine) from near the coasts only, suggests a need for further and more intensive collecting throughout the world.

Methods

Methods of counting and measuring generally follow those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). All measurements are in mm, and body proportions (Table 1) are in percent of total length. Features used in measuring and counting are shown in Figures 1 and 2, and geographic distribution in Figure 3. Counts of slime pores (Tables 2–5) and unicusps (Table 6) represent the left side only because we have found no significant differences between the left and right sides. Occasionally one extra gill pouch occurs, usually on one side only and much smaller than normal; one less pouch rarely occurs on either side. The one to three slime pores which may occur over the pharyngocutaneous duct are included in the prebranchial pore count. In all species of *Myxine* only two fused cusps (a multicusp) occur on the posterior set of cusps (inner row of Fernholm and Hubbs, 1981) in contrast to either two or three on the anterior set. This latter character is used to group species (Tables 1–7). Some terms have appeared previously in myxinid accounts without clear definition. We offer precise definition of these and some new terms used in this study: **rostrum**, rounded to pointed, fleshy extension lying over the nasal orifice between the anteriormost pairs of barbels; **head**, from tip of rostrum to a vertical from wrinkled tissue below the mouth; **face**, ventral aspect of head; **mouth,** the elongate slit in face which opens to permit extrusion of cusps for feeding (Fig. 2A); **multicusp**, a unit of two or three cusps (teeth of other authors), fused together at bases (Fig. 2B); **unicusp,** a single unfused cusp (Fig. 2C); **pores** (slime pores), the small openings along the ventral aspect of body which emit mucus; **gill aperture** (GA), the opening through which water discharges to the exterior after passing through the gill pouches; **PCD,** the external opening of the pharyngocutaneous duct, always on the left side and usually confluent with the left gill aperture in *Myxine* (or posteriormost GA in *Eptatretus*); **ventral finfold** (VFF), a band of thin, fleshy tissue extending along ventral midline of body between PCD and origin of cloaca (Fig. 1); **cloaca**, the slit-like ventral opening anterior to tail through which body wastes and sexual products discharge; and **caudal finfold** (CFF), the band of thin fleshy tissue extending around tail, ending dorsally about over origin of cloaca (Fig. 1).

Colors are determined after scraping away the coating of coagulated slime (mucus). Although given in the descriptions, color is subjective and may change greatly with preservation; therefore, the use of counts is preferred as a more distinguishing character. Because eggs are similar in all species, we have not used them as a species character. They vary widely in length and diameter and in developmental stages, ranging from tiny to nearly mature in females of the same length. Accurate measurement of diameter is hindered in eggs deformed because of crowding in life or during preservation; many are somewhat flattened and diameters may vary as much as 1.5 mm in the same specimen. We have not provided photographs or drawings of individual species since

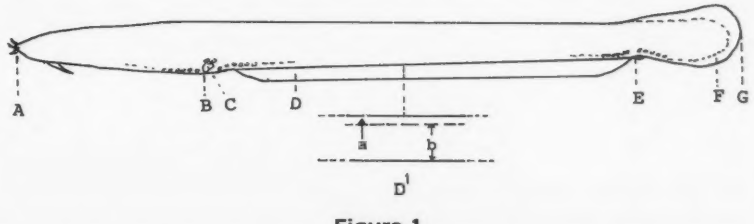

Figure 1

Sketch of a *Myxine* showing features used in measuring and counting: A–G = total length (TL); A–B = prebranchial length; C = opening of the pharyngocutaneous duct (PCD); D = ventral finfold (VFF), D´= enlarged portion of VFF with dashed line indicating the approximate difference between a well and a weakly developed VFF; E = origin of cloaca; E–G = tail length; F = caudal finfold (CFF). The many slime pores along the sides are indicated by a few small circles near PCD and cloaca.

there are no distinguishing external features other than those characters given in the key. A list of the materials examined and of the collections where these materials were obtained follows the Acknowledgment section. Institutional abbreviations are listed as in Leviton, et al. (1985).

Key to new world hagfishes (Genus *Myxine*)

1a A 3-cusp multicusp on anterior set, a 2-cusp multicusp on posterior set of cusps **2**
1b A 2-cusp multicusp on both the anterior and posterior sets of cusps **6**

2a Gill pouches 6, rarely 7 ..... **3**
2b Gill pouches 5 ..... **4**

3a VFF well developed, 3–7 mm high, mounted on thick triangular base extending from the ventral surface; last few prebranchial pores in an uneven line, resembling the letter W; total pores 112–121 ..... ***M. fernholmi***
3b VFF vestigial, not mounted on triangular fleshy base; last few prebranchial pores in a straight line; total pores 103- 104 ..... ***M. debueni***

4a Anterior unicusps 6–9; total cusps 36–48; total pores 77–92; color light brown, often lighter dorsally than ventrally ..... ***M. mccoskeri***
4b Anterior unicusps more than 9 each side **5**

5a Anterior unicusps 11–13; total cusps 56–58; total pores 92–100; VFF usually low (3–6 mm); head and barbels pale ..... ***M. robinsi***
5b Anterior unicusps 7–13; total cusps 43–56; total pores 80–102; VFF usually prominent, averaging 5 mm (1–12 mm); head and barbels usually pale ..... ***M. circifrons***

6a Gill pouches 7; anterior unicusps 4; posterior unicusps 5–6; total cusps 26–28 ..... ***M. pequenoi***
6b Gill pouches 6, rarely 7 ..... **7**

7a CFF extending forward dorsally 2–3 times tail length; total pores 108–109; VFF low, (3–5 mm) ..... ***M. dorsum***
7b CFF not extending forward dorsally much beyond a vertical above cloacal origin **8**

8a Prominent whitish band on ventral surface; VFF usually well developed **9**
8b No prominent ventral whitish band **10**

9a Ventral whitish band not extending above line of trunk pores, but often extending to face; color dark reddish-brown; total cusps 38–46 ..... ***M. affinis***
9b Ventral whitish band extending above line of trunk pores, often increasing as wide blotches between GA and face; body brown to purplish; total cusps 29–38 ..... ***M. australis***

10a VFF moderately to well developed **11**
10b VFF vestigial, or nearly so **12**

11a Color bluish gray to brownish, head pale; whitish mid-dorsal narrow stripe extending forward a variable distance; total cusps 42–48; total pores 101–119 ..... ***M. mcmillanae***
11b Color pinkish-brown to various shades of purple, often dark; head usually pale; narrow whitish streak of variable length extending along dorsal midline from CFF; total cusps 30–49; total pores 89–118 ..... ***M. limosa***

12a VFF nearly vestigial, 1–3 mm high; color pinkish to bluish; head pale; prebranchial pores 31–32; trunk pores 61–65; total pores 108–110 ..... ***M. knappi***
12b VFF vestigial; color brown to purplish-black; prebranchial pores 18–31; trunk pores 58–72; total pores 91–116 ..... **13**

13a Color light to dark purplish-brown; occasional pale blotches ventrally; total pores 101–109; VFF variably vestigial to 8 mm high ..... ***M. hubbsi***
13b Color dark brown to blackish; no pale blotches ventrally; head only slightly pale; total pores 111–116; VFF vestigial, intermittently absent ..... ***M. hubbsoides***

Systematics

Myxine circifrons Garman, 1899

Myxine circifrons Garman, 1899: 344 "Albatross Station 3395; 7°30'36"N, 78°W; 730 fm (1,336 m) temperature 38.5°F; bottom rocky."

Diagnosis A 3-cusp multicusp on anterior sets of cusps; five gill pouches each side; color blackish to dark reddish-brown, anteriormost portion of head pale.

Description Counts and proportions are given in Tables 1–7. Body robust, slightly deeper than wide; snout bluntly pointed, rostrum short, variably triangular to bluntly rounded; cusps short, stout; anterior multicusps bulbous at bases, the free tips about equal in length to bulbous portion; tail length about 13% of TL, its depth about 40% of its length; VFF usually well developed, but may be vestigial, ranging in height from 1 to 12 mm, averaging about 5 mm; CFF high, extending around tail to about over cloaca, thickened dorsally; body color dark, grayish-black to reddish-brown; anterior portion of head paler, often whitish to near vertical from margin of face, occasionally extending into the prebranchial region; barbels color of head; VFF and CFF same color as body, without pale margins; GA and slime pores often with narrow pale margins; total cusps 43–56; total slime pores 80–102; numbers of large eggs (20 mm and longer) range from 15 to 18 in females of 435 mm TL, largest egg 28 × 7 mm.

Distribution From near San Francisco, California, to north-central Chile at depths of about 700 to 1,860 m (Fig. 3). We find no significant differences in counts or proportions throughout this extensive range of about 11,000 kilometers.

Comments Sex ratios in our material are equal off southern California (n=220) but unequal near the mouth of the Gulf of California (n=136), 66% female to 34% male, and Costa Rica to northern Chile (n=54), 59% female to 41% male. We find no hermaphrodit-

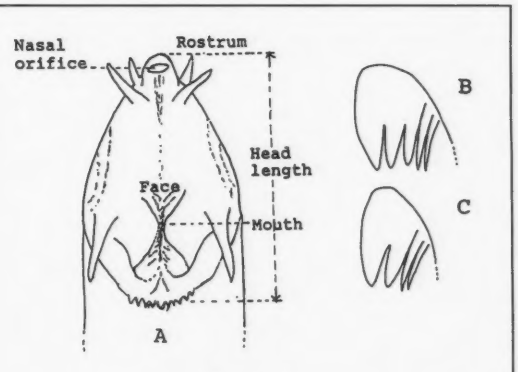

Figure 2

(**A**) sketch of ventral aspect of a myxinid head, identifying the terms used in the text: (**B**) and (**C**), sketches of a 3-cusp and a 2-cusp multicusp, with two adjacent unicusps.

Figure 3

Areas of occurrence of new world species of Myxine: 1 = *M. circifrons*, from near San Francisco, California, to north-central Chile; 2 = *M. hubbsi*, from near San Francisco, California, to near Valparaiso, Chile; 3 = *M. hubbsoides* and 4 = *M. pequenoi*, off south-central Chile; 5 = *M. fernholmi*, from near Valdivia, Chile to Falkland Islands, S.E. Atlantic Ocean; 6 = *M. dorsum* and 7 = *M. debueni*, Straits of Magellan; 8 = *M. australis*, principally in Straits of Magellan; two collections off Chile, and one near Pta. Nuevo, Argentina; 9 = *M. affinis*, Straits of Magellan; 10 = *M. knappi*, near the Falkland Islands; 11 = *M. mccoskeri*, 12 = *M. robinsi*, and 13 = *M. mcmillanae*, southern Caribbean Sea; 14 = *M. limosa*, Davis Strait, Greenland, southerly to eastern portion of the Gulf of Mexico.

ism in 320 specimens exceeding 350 mm TL, a minimum length arbitrarily chosen as offering reliable sex determination.

Myxine mccoskeri new species

Holotype SIO70-363, female, 201 mm, taken at 09°39'N, 78°60'W, 530–560 m, 1 October 1970.

Paratypes SIO70-363, 2 (117, 170 mm), taken with the holotype; SIO90-117, 1 (235 mm), 11°46'N, 67°05'W, 1, 100–1,174 m (formerly UMML 29269); USNM 325212, 2 (170, 235 mm), 11°30'N, 72°26'W, 530–567 m (formerly UMML 28722); CAS 79537, 2 (170, 235 mm), 12°13'N, 75°50'W, depth unknown (formerly UMML 29884); MCZ 48809, 2 (218, 264 mm), 11°35'N, 62°52'W, 512–547 m; MCZ 41634, 1 (254 mm), 11°35'N, 62°59'N, 439–476 m.

Diagnosis A 3-cusp multicusp on anterior sets of cusps; five gill pouches each side; VFF weakly developed, often nearly vestigial, 0–5 mm high; color dark brown, often lighter dorsally than ventrally; a dwarf species, mature at about 300 mm TL.

Description Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide, its width about 75% of its depth; tail narrow, its length about 15% of TL, its depth about 33% of its length. VFF usually low, ranging in height from 0–5 mm, average 2 mm; CFF prominent, its margins thin, the internal supporting rays visible; snout rather sharply pointed, rostrum elongate, bluntly pointed; cusps long, slender, sharp, the bases of multicusps slightly bulbous; body variably pale to medium or dark brown, the head and ventral aspects anterior to GA lighter than body; posterior to GA the ventral aspect is notably darker toward end of tail, a pale band extends dorsally to over the cloaca, the general aspect being reverse countershading; VFF and CFF color of body, usually without, or with faintly expressed, pale margins; barbels very slightly or not at all pigmented; GA with narrow pale margins, slime pores without; total slime pores 77–92; total cusps 36–48. A 264-mm-TL paratype (MCZ 48809) contains only four large eggs, each about 18×7 mm; in addition, two other females (218, 222 mm) contain four and five eggs, about 15×5 mm. We consider this species dwarfed because of the short length of females with such large eggs.

Etymology We name this species for John E. McCosker, Director, Steinhart Aquarium, San Francisco, for his work on Caribbean and Panamanian fishes, and for making the first specimens of this species available to us.

Distribution Known only from the southern Caribbean Sea (Fig. 3).

Comments Shimizu (1983) reported as *Myxine* sp. three specimens (273–320 mm TL) from off Suriname at 310 m, with 3-cusp multicusps on anterior sets of cusps, 38 total cusps, and 87–90 total slime pores; number of gill pouches and sexual maturity not stated. Color was described as "Body color white on snout, gradually becoming blackish, and uniformly black behind posterior half of head." The cusp and slime pore counts agree well with *M. mccoskeri*; however, the white snout as described and shown in the color photo from Shimizu, is whiter than those on our specimens of *M. mccoskeri*. This feature and the blackish body are more like those of *M. robinsi* (described below); however, the latter has more total cusps (56–58) and total pores (94–104).

Myxine robinsi new species

Holotype SIO90-149, ripe female, 475 mm TL, taken at 11°37'N, 60°50'W, in a 40-ft otter trawl between 783 and 1281 m (formerly UMML 29270, date of capture not recorded).

Paratypes SIO90-149, 1 (510 mm) taken with the holotype; USNM 325213, 1 (540 mm); 11°37'N, 60°59'W (formerly UMML 29877); MCZ 101239, 1 (460 mm), 10°03'N, 7620'W, (formerly UMML 22807), 675–966 fm [1,235–1,768 m].

Diagnosis A 3-cusp multicusp on anterior set of cusps; five gill pouches each side; whitish on head and continuing to first few prebranchial pores, and light dorsally to about over GA; body light to medium brown.

Description Counts and proportions are given in Tables 1–7. Body rather robust, slightly deeper than wide; tail length about 13% of TL, its depth about 38% of its length; VFF moderately well developed, 3–6 mm high; CFF prominent, extending around tail to about over cloacal origin, thickening dorsally; rostrum variably rounded to bluntly conical; anterior unicusps long, slender, sharp, curved near tips; bases of anterior multicusps slightly bulbous; color light to medium brown; head whitish continuing to first few prebranchial pores; a decreasingly paler area, often blotchy, extends posteriorly along dorsal surface and often laterally to near GA; slime pores and GA with no or very pale margins; VFF and CFF color of body, without pale margins. One female 475 mm TL contains six large eggs, 29–31 mm long by 11–12 mm wide, arranged in a single row.

Etymology We name this new species for both C. Richard and Catherine Robins, University of Miami Rosenstiel School of Marine and Atmospheric Sciences, for their works on the marine fauna of the tropical western Atlantic, particularly the Caribbean area.

Distribution Known only from the type material from the southern Caribbean Sea (Fig. 3).

Discussion *Myxine circifrons, M. mccoskeri,* and *M. robinsi* may be closely related. Each has a 3-cusp multicusp on the anterior sets of cusps and are the only species of *Myxine* known to have only five gill pouches each side. Counts and most body proportions overlap, which invites speculation that prior to the permanent establishment of the Panamanian land barrier, *M. circifrons* may have occupied the Caribbean area. If true, *M. robinsi* evolved primarily to a lighter color and *M. mccoskeri* to a dwarfed state, with fewer anterior unicusps, trunk and total slime pores, as well as a strikingly different color pattern. All counts for *M. robinsi* are similar to those for *M. circifrons.* However, despite these similarities, we hold *M. mccoskeri* and *M. robinsi* to be specifically distinct from *M. circifrons.* Although *Myxine mcmillanae* is also from the same area (see below), we do not consider it related because it has a 2-cusp multicusp on both anterior and posterior sets of cusps and six gill pouches rather than five. One other species with 3-cusp multicusps on anterior row is *M. garmani,* known only from Japan and distinct from the three species described above that have six gill pouches rather than five and a wide geographical separation.

Myxine fernholmi new species

Holotype ISH 257-1978, female, 555 mm TL, taken at 49°29'S, 58°56'W, 200-ft bottom trawl, 400 m, 6 June 1968.

Paratypes SIO90-138, 1 (790 mm), 53°00'S, 64°00'W (formerly ISH 108–1971); SIO90-139, 1 (575 mm), 33°39'S, 72°09'W, 1,170–1,480 m; ZIL 791–966, 1 (665 mm), 54°35'S, 57°30'W, 135–145 m.

Diagnosis A 3-cusp multicusp on anterior sets of cusps, total cusps 34–37; six gill pouches each side; tail length 10% or less of TL; last four prebranchial pores forming an irregular line which resembles the letter *W.*

Description Counts and proportions are given in Tables 1–7. Body moderately robust, slightly deeper than wide; tail short, 8–10% of TL, its depth about half its length; VFF extending 3–7 mm, and mounted on a prominent fleshy triangular extension along the ventral surface; CFF thin, high, extending around tail to about over cloacal origin; reddish supporting rays visible on most specimens; rostrum triangular, the tip slightly rounded; unicusps long, slender, sharp, slightly curved at tips; bases on anterior multicusps bulbous, posterior multicusps not bulbous; last four prebranchial slime pores anterior to GA in an irregular line forming a pattern resembling the letter *W*; all slime pores tiny; tail pores 7–9, total slime pores 112–121; color variably pale, yellowish, or light bluish-pink; GA with prominent pale margins, slime pores with less prominent; females with only immature eggs, 2–8 mm long.

Etymology We name this species for Bo Fernholm, Museum of Natural History, Stockholm, for his work on the physiology, anatomy, and systematics of Myxinidae.

Distribution Known only from the type material taken off south- central Chile and near the Falkland Islands, southwestern Atlantic Ocean (Fig. 3).

Myxine debueni new species

Holotype SIO90-140, male, 570 mm TL, taken at 53°39'S, 70°14'W, 300 m, 27 April 1970, Straits of Magellan.

Paratype SIO90-140, male 545 mm TL, taken with the holotype.

Diagnosis A 3-cusp multicusp on anterior sets of cusps; six gill pouches each side; VFF absent; tail short, 8–9% of TL; rostrum triangular, the tip pointed; prebranchial slime pores in a straight line anterior to GA.

Description Counts and proportions are given in Tables 1–7. Body slender, nearly cylindrical; tail short, 8–9% of TL; depth about 40% of length; VFF absent; CFF prominent, thickened at margin, extending around tail to over cloacal origin; head narrow, pointed, rostrum triangular, the tip pointed; unicusps long, slender, sharp, slightly curved; bases of multicusps not bulbous; prebranchial slime pores in a straight line anterior to GA. The two specimens appear to have been "dry-burned" from insufficient preservative, causing the skin to harden and become a dark reddish-brown color on damaged portion, mostly dorsally. Undamaged part of body is pale bluish-gray anterior to GA; posteriorly a pale pinkish color continues to tail; CFF with narrow pale margins, slime pores with very narrow ones.

Etymology We name this species for Fernando DeBuen in recognition of his extensive work on fishes of South America.

Distribution Known only from the two specimens from the Straits of Magellan (Fig. 3).

Comments This species and *M. fernholmi* (described above) are similar in that each has a tail length of 10% or less of TL and a somewhat longer trunk length than other species treated here. Each has a 3-cusp multicusp on the anterior sets of cusps; they differ primarily in *M. debueni* lacking a VFF (prominent in *M. fernholmi*); also, the last four prebranchial pores lie in a straight line not forming the letter *W*.

Myxine hubbsi new species.

Synonymy *Myxine circifrons* Chirichigno, 1968:383 (description; a 2-cusp multicusp on anterior set of cusps; northern Peru to Gulf of Panama).

Holotype SIO65-452, female, 515 mm TL, taken at 32°38'N, 118°08°4'W, 25 September 1965, bottom trap, 2,009 m.

Paratypes SIO65-452, 82 (209–522 mm), taken with the holotype; SIO68-60, 36 (120–484 mm), 23°07'N, 109°16'W, 1,830 m; SIO68-61, 2 (350, 400 mm), 23°06'N, 109°13'W, 2,196 m; SIO73-293, 16 (230–480 mm), 09°24'N, 85°06'W, 1,107 m; SIO92-114, 7 (260–450 mm), 03°41'S, 81°36'W, 2,440 m; SIO92-115, 7 (290–420 mm), 08°26'S, 80°36'W, 1,830–1,930 m; SIO72-176, 8 (326–473 mm), 21°37'S, 70°55'W, 2,114 m; CAS 79536, 10 (280–445 mm), taken with the holotype, CAS 77360, 3 (322–410 mm), 31°00'N, 118°06'W, 1,739 m (formerly SIO65-451); LACM 45786-1, 18 (222–456 mm), 32°40'N, 118°12'W, 1,742 m (formerly SIO65-451); USNM 325214, 16 (258–486 mm), 32°39'N, 118°11'W, 1,830 m, (formerly SIO68-676); MCZ 101240, 6 (275–460 mm), 32°41'N, 118°12'W, 1,823 m.

Diagnosis A 2-cusp multicusp on both anterior and posterior sets of cusps; six gill pouches each side (very rarely 5 or 7); body nearly cylindrical; VFF low to vestigial; rostrum rounded; color light to dark brownish-purple to nearly black; head and barbels pale.

Description Counts and proportions are given in Tables 1–7. Body nearly cylindrical, its width narrowing posteriorly; tail length about 10% of TL, its depth about 38% of its length; VFF weakly developed, often vestigial or absent. Of 205 specimens, 155 (75%), VFF ranges in height between 3 and 4 mm, and between 6 and 8 mm in only 4 specimens; CFF well developed, often thick at margin, ending over cloacal origin; head bluntly pointed, rostrum short, rounded; multicusps small, short, bulbous at bases; unicusps slender, sharp; body color variably light to dark purplish-black, rarely with pale blotches; head usually pale anteriorly; all barbels pale; VFF and CFF color of body; GA with narrow pale margins; slime pores only occasionally with pale margins. From 7 to 15 large eggs, ranging between 17×6 and 24×8 mm, occur in eight females (415–450 mm TL); all other females have small eggs. The largest number of eggs (15) occur in a female of 440 mm TL.

Etymology We name this species for our deceased friend and mentor Carl L. Hubbs, primarily for his foresight in instigating the worldwide study on hagfishes.

Distribution Known from 33°N to 34°S, at depths from about 1,100 to 2,440 m (Fig. 3). As in *M. circifrons* (discussed above), we find no significant differences in counts or proportions over this range of about 9,000 km.

Comments The sex ratio in our material is extremely unbalanced; of 150 specimens, 114 (76%) are female, 35 (23%) hermaphroditic, and 6 (0.4%) male. Although there were few large eggs (7–15), no eggs were lost since no specimens were opened prior to our examination. Bichromatism is rare; only five of 36 specimens from near Cape San Lucas, Baja California, Mexico (SIO68-60), are notably bichromatic with colors generally bluish-purple ventrally and laterally, the dorsal areas pinkish. Most bodies are pale anterior to GA, with occasional small to large bluish blotches; similar bichromatism occurs in five of nine specimens off San Diego, California.

Myxine hubbsoides new species

Holotype SIO90-143, hermaphroditic female, 826 mm TL, taken at 34°00'S, 72°14'W, 880 m, formerly MNHMC 80047).

Paratypes SIO90-141, hermaphroditic female, 702 mm TL, 34°21'S, 78°18'W, 820 m (formerly MNHMC 80043); SIO90-142, female, 651 mm TL, 34°14'S, 72°21'W, 735 m (formerly MNHMC 80044).

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; VFF vestigial or nearly so, often absent; total pores 111–116.

Description Counts and proportions are given in Tables 1–7. Body slender, cylindrical; tail length about 12% of TL, its depth about 35% of its length; VFF very low, portions intermittently absent; CFF variably well developed, ranging between thick at cloaca and around tail to thin dorsally, ending about over cloaca; rostrum broadly rounded at tip; all cusps in anterior sets bulbous at bases, those of posterior sets not bulbous; all unicusps straight or only slightly curved; body color blackish-brown with no pale areas or spots; head only slightly paler; face pale to slightly past mouth; barbels almost entirely pale; GA and slime pores with very narrow pale margins. The 702-mm paratype (SIO90–141) has 49 dark brown eggs as large as 17×5 mm, with many tiny round eggs scattered among them; the holotype has many eggs to about 11 mm, but was not opened fully for count; well-developed testicular tissue present posterior to eggs; the 651-mm paratype is spent or immature and has very few tiny eggs present.

Etymology The name *hubbsoides* refers to the similarity to *Myxine hubbsi* described above.

Distribution Known only from off central Chile between Coquimbo and Punta Topocalma (Fig. 3).

Myxine pequenoi new species.

Holotype SIO90-145, 183 mm TL, maturing female, taken at 41°29'S, 74°09'W, 185 m.

Paratype SIO90-146, 175 mm TL, mature male, taken at 40°44'S, 74°14'W, 215 m.

Diagnosis A 2-cusp multicusp on both anterior and posterior sets of cusps; total cusps 26–28; seven gill pouches each side; VFF nearly vestigial; total slime pores 81–85; a dwarfed species.

Description Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide; tail about 12% of TL, its depth about 30% of its length; VFF very low; CFF thick at margin, thinner around tail, ending well behind a vertical from origin of cloaca; rostrum short, sharply pointed; barbels small, pale; all cusps have bulbous bases, with sharp, slender points; seven gill pouches; head and body medium brown, lighter ventrally; GA and slime pores with narrow pale margins; VFF and CFF with pale margins; holotype with 10 maturing eggs to 10×4 mm; most eggs in a single row; paratype with well-developed testes. We regard this species as dwarfed because of the advanced sexual development of these two small specimens, 175 and 183 mm TL (even smaller than *M. mccoskeri* described above).

Etymology We name this species for German Pequeño R., Instituto de Zoologia, Universidad Austral de Chile, Valdivia, for his work on the fishes of Chile and for making specimens available to us.

Distribution Known only from the type specimens taken south of Valdivia, Chile, about 41°S, 74°W (Fig. 3).

Discussion Within the genus *Myxine,* only three species have seven gill pouches (except rarely in *M. hubbsi* and *M. mcmillanae*). These three are *M. capensis* Regan, 1913, from off South Africa (22° to 25°S, 16°17°W), *M. ios* Fernholm, 1981, from southwest of Ireland (40° to 41°N, 12° to 13°W) and *M. pequenoi* (described above) from off Chile. Proportions of the three species are quite similar despite the dwarfed condition of *M. pequenoi*, but significant differences occur in certain counts. Those for *M. pequenoi* are given first followed in parentheses by those for *M. capensis* and *M. ios.* Total cusps 26–28 (36–43, 44–49); prebranchial slime pores 22–23 (26-28–28–36); total slime pores 81–88 (92–110, 103–117). Body colors are similar in all three species except that *M. ios* from near Ireland has a white head; the others do not. *Myxine paucidens* (known only from Japan) has the same number of unicusps as *M. pequenoi* (4 on anterior and 5 on posterior sets of cusps) but is distinctly different with six gill pouches, as well as having wide geographical separation.

Myxine dorsum new species

Holotype ISH 99-1971, 440 mm female, taken at 54°25'S, 59°42'W, 140-ft bottom trawl, 112 m.

Paratype SIO92-21 (formerly ZIN 722–966), 490 mm female, taken at 49°16'S, 57°02'W, bottom trawl, 630–650 m.

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches; VFF low, 2.0 mm high; CFF extending forward dorsally as a ridge beyond a vertical from cloacal origin three to four times the length of tail; total slime pores 108–113; color light pinkish-brown.

Description Counts and proportions are given in Tables 1–7. Body moderately slender, slightly deeper than wide; tail about 13% of TL, its depth 40% of its length; VFF low, 2.0 mm, mounted on a prominent fleshy narrow triangular base extending 4–7 mm from body and defined by an intermittent suture-like line below the rows of pores; a structure similar to that of *M. fernholmi* (described above) but much less strongly developed; CFF wide, thick ventrally, thin-

ning around tail and dorsally; prominent dorsal ridge extending anteriorly as a finfold to 4.3 times tail length in holotype and 3.2 times in paratype; body light pinkish-brown, the original label states "life-long color pink"; VFF and CFF pale; GA and slime pores with narrow pale margins; holotype with 9 well-developed eggs to 19×5 mm; paratype with 8 similar eggs to 18×6 mm; eggs widely and irregularly spaced; only a few paired.

Etymology The name *dorsum,* from Latin meaning "ridge," refers to the far forward extension of the CFF dorsally as a ridge to three or four times length of tail.

Distribution Southwestern Atlantic Ocean between 112 and 650 m (Fig. 3).

Discussion Although the two specimens are slightly wrinkled and hardened, the integuments cannot be stretched laterally and down far enough to eliminate the dorsal ridges. In addition, a suture-like line parallels the base of these ridges, ending at the point where downward stretching fails to eliminate them. This feature is not previously reported in species of *Myxine;* in all others, CFF extends dorsally little more than half a tail length forward of a vertical from cloacal origin.

Myxine knappi new species

Holotype SIO90-144, 565-mm female, taken at 49°16'S, 57°02'W, 24 March 1965, 630–650 m.

Paratypes SIO90-144, 2 (510,560 mm TL) taken with the holotype.

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; tail slime pores 11–14; rostrum broadly rounded; VFF nearly vestigial; color pinkish-blue, head and barbels slightly paler than body; total slime pores 116–123.

Description Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide; tail length about 13% of TL, its depth about 33% of its length; VFF low and variably developed; in the holotype it is 2.5 to 3.5 mm high; in a paratype (510 mm TL) it is less than 1.0 mm high to about 60 mm anterior to cloaca where it increases to 3.0 mm high, continuing to cloaca; CFF prominent around tail, thickened ventrally; in the 510 mm paratype CFF extends forward of a vertical from cloacal origin about half the tail length; rostrum broadly rounded at tip; cusps robust, bluntly pointed, bases of multicusps slightly bulbous; 1–2 slime pores over GA; body color pinkish to bluish, one paratype more pink than blue; head pale to about over mouth; barbels pale; VFF entirely pale; CFF color of body, without pale margin; GA and slime pores with narrow pale margins; a label in the package containing the bluish specimen states "life-long color blue." The pinkish specimen was packaged separately with label stating "life-long color pink"; holotype with 15 large eggs to 26×7 mm; pink paratype with 12 eggs as large as 18×6 mm.

Etymology We name this species for Leslie W. Knapp, Director, Department of Fishes, Smithsonian Sorting Center, primarily for supplying us with study material.

Discussion This species and *M. dorsum* appear to be closely related, differing primarily in far forward extension of CFF in *M. dorsum;* this feature is weakly expressed in a paratype of *M. knappi* by an extension of about half the tail length.

Distribution Known only from near the Falkland Islands (Fig. 3).

Comments A discrepancy exists in recorded dates of capture. The "life-long pink" specimen has a label stating the date of capture as "March 24, 1935"; the label with the two "life-long blue" specimens (packaged separately) states "March 24, 1965." All other data, handwriting, and label paper are identical; therefore we assume the date of 1935 to be in error because we know of no Russian research vessel collecting near the Falkland Islands in 1935. Because of the poor condition of one of the paratypes, it was not possible to obtain accurate body measurements or slime pore counts; however, we were able to count the cusps.

Myxine australis Jenyns, 1842

Myxine australis Jenyns, 1842:159 (description: "colored like an earthworm but more leaden, beneath yellowish, head purplish; Tierra del Fuego").

Synonymy *Myxine acutifrons* Garman, 1899:347 (from original description: rostrum acute, resembling a barbel; color dark brown, lighter ventrally; anterior two teeth of each series confluent to bases).

Diagnosis 2-cusp multicusp on both anterior and posterior sets of cusps; six gill pouches each side; head pointed, rostrum variably acute to rounded at tip; VFF low, averaging less than 2 mm; CFF narrow; a

wide yellow ventral band extends slightly above rows of slime pores, continuing in a variably wide band to the yellow face.

Description Counts and proportions are given in Tables 1–7. Body slightly deeper than wide; tail slender, width about 33% of its length, its length 15% of TL; head narrow, pointed; tip of rostrum variably acute to rounded; a 2-cusp multicusp on both the anterior and posterior sets of cusps; VFF usually low, 0–6 mm, averaging 1.6 mm; CFF thin and wide around slender tail; body color reddish to dark brown, top of head dark; prominent yellow band ventrally extending slightly above rows of slime pores, continuing forward and widening into large blotches anterior to GA and to yellow face; large eggs range in numbers and sizes between 9 (24×8 mm) in a 330 mm female, and 16 (21×7 mm) in one of 345 mm TL.

Distribution Principally in and near the Straits of Magellan; however, three collections are from farther north (two off Argentina: 48°18'S, 65°06'W, and 50°00'S, 68°30'W, and one off Chile at 48°29'S, 78°46'W). Frequently taken with *M. affinis* (Fig. 3).

Comments The sex ratio of our material is unbalanced: of 86 specimens, 71 are female, 12 male, and 3 hermaphroditic. Although the multicusp pattern and number of gill pouches is the same as *M. affinis*, *M. australis* may be distinguished by fewer unicusps, fewer trunk and total pores, and shorter TL of mature specimens.

Myxine affinis Günther, 1870

Synonymy *Muraenoblenny olivacea* Lacépède, 1803: 6524 ("olive without spots, ventral surface whitish; no pectoral fins, no appearance of other fins; copious slime production"); presumably from the Straits of Magellan [nomen dubium].

Myxine affinis Günther, 1870, Catalog 8:511 ("Eleven rather stout teeth in each of two series, the foremost strongest and more confluent at the base than the others. Hab._____? Twelve inches long") Norman, 1937:2–8 (examination of type; 11 teeth in each series; body too dried and hardened for slime pore counts).

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; VFF variably developed; color reddish-brown to purple.

Description Counts and body proportions are given in Tables 1–7. Body slightly deeper than wide; rostrum triangular, tip rounded; barbels dark at base, pale distally; VFF yellowish , usually low, averaging 3 mm, but ranging from 0.5 to 13 mm, only 3 specimens with VFF between 8 and 13 mm; CFF wide, rarely with pale margin; tail about 15% of TL, its depth about 38% of its length; body reddish-brown to purple, head region somewhat lighter; narrow yellow band ventrally limited to below the lines of pores, often extending as intermittent patches to the yellowish face; GA and slime pores with narrow pale margins; numbers and sizes of large eggs range from 36 (20×6 mm) in a female of 550 mm TL to 17 (26×9 mm) in one of 475 mm TL.

Distribution Within or closely adjacent to the Straits of Magellan (Fig. 3).

Comments Frequently taken with *M. australis* but distinguished by higher unicusp and trunk slime pore count, as well as by generally larger eggs and a longer body. Sex ratio of our material is unbalanced; of 256 specimens sexed, 171 (67%) are female, 48 (19%) male and 37 (14%) hermaphroditic.

Myxine mcmillanae Hensley, 1991

Myxine mcmillanae Hensley, 1991:1040–1043.

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches (rarely seven) each side; color dark bluish-gray to brown; head whitish to first slime pores.

Description Counts and proportions are given in Tables 1–7. Body slightly deeper than wide; tail length 13% of TL, its depth 40% of its length; of 43 specimens two have seven pouches on the left side, one has seven on right side; VFF 3–6 mm high; body dark bluish-gray to brown; head pale to first slime pores; rostrum triangular, rounded at tip; VFF, CFF and margins of PCD, GA and slime pores pale; 7 to 11 large eggs (27–36 by 8–9 mm); the polar caps weakly developed.

Distribution Known only from the Caribbean Sea, west and southwest of Puerto Rico and from St Croix, U.S. Virgin Islands (Fig. 3).

Comment Hensley (1991) did not report on the sex of his material. The 10 specimens available to us (SI090-21) were all females. No hermaphroditism was noted.

Myxine limosa Girard, 1858

Myxine limosa Girard, 1858:223–224. (abundance: Grand Manan Isle; Bay of Fundy; 50 fm).

Synonymy *Myxine atlanticus* Regan, 1913:398 (Western North Atlantic, 44°27'N, 58°10'W; 120 fm; counts, proportions).

Diagnosis A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; head rather pointed, rostrum triangular, bluntly pointed; color reddish-brown to dark purple; head often pale; occasional ventral blotches; VFF variably low to high; a narrow pale streak on dorsal midline usually present.

Description Counts and body proportions are given in Tables 1–7. Body slender, nearly cylindrical; tail slender, 12–17% of TL, its depth about 30% of its length; VFF low, 0–4 mm (average 1.6 mm); CFF prominent, thin, thickening dorsally; head pointed, rostrum bluntly triangular; body color varying shades of reddish-brown to blackish-purple; head only slightly pale; occasional pale blotches ventrally; VFF and CFF usually with pale margins; GA and slime pores with prominent pale margins; a narrow pale streak of variable length usually present on dorsal midline; females (368–385 mm TL) contain 12 to 20 large eggs, 17×5 to 27×8 mm; a 385 mm female contains 14 fully developed eggs, 16×6 to 17×8 mm, all linked by anchor filaments.

Distribution Between Davis Strait (66°N) and south to Florida, between 75 and 1,006 m; one specimen (383 mm TL) from Campeche Bank, Gulf of Mexico, at 24°25'N, 87°38'W.

Discussion Since its description, *M. limosa* has often been identified as *M. glutinosa* L. (1758) from the eastern North Atlantic (ENA), but we find two characters involving coloration that distinguish the two. All descriptions and our findings on ENA material indicate a grayish-pink color; in contrast, all our western North Atlantic (WNA) material is reddish-brown to blackish-purple. Girard (1858) indicated reddish to dark brown or black. In addition to the much darker coloration, most WNA specimens have a narrow pale streak along the dorsal midline extending forward from CFF an average of 46% (18–80% of TL). This pale streak is not mentioned by any author offering color descriptions of WNA material, and it is not present in ENA material available to us (180 from Skagerrak, Denmark; SIO59–50). This streak appears to result from white connective tissue binding skin to the dorsal midline in conjunction with an overlying unpigmented streak in the skin. Removal of the overlying skin and examination with the aid of strong backlighting shows this band to be present only in WNA material. Also, a difference in maximum lengths exists between mature specimens of *M. limosa* and *M. glutinosa*. Of 250 specimens of the former, the longest is 510 mm TL, and 133 exceed 400 mm, averaging 445 mm TL. Tambs-Lyche (1969:283) reported "maximum 450 mm" for ENA material. Conel (1917:78) recorded a maximum length of 79 cm from off South Harpswell, Maine, and stated that of 20 specimens, only three were between 31 and 36 cm; all others were from 50 to 79 cm. We have not seen any that large, and no further description of the 20 specimens was given.

Comments Apparently all previous authors have assumed that *M. glutinosa* occurs across the North Atlantic Ocean, but Saemundsson (1949) did not include it in his list of fishes from Iceland. However, Konstantinov and Shchegelov (1958:1745) stated "On June 16, 1956, near the eastern coast of Iceland, at the depth of 940 m, a *M. glutinosa* L., 28.5 cm long, was caught in a Sigsbee trawl." We consider these two species closely related, and have included *M.glutinosa* in all the tables for comparison with *M. limosa*.

Discussion

Owing to the absence of a fossil record, we are unable to state with certainty whether or not the new world species treated herein are monophyletic or polyphyletic. However, monophyly is assumed, based on the synapomorphic character of having all branchial ducts on either side combined into one single external opening posterior to the gill pouches. Also, monophyly of *Myxine* is supported by allozyme studies of hagfish from three continents.[1]

Relationships among these 14 species are in general somewhat obscure on the basis of body proportions and most counts. Although some means differ (Tables 1–7), considerable overlap in ranges of counts tends to mask significance. Only two species (both new) differ notably in body proportions (Table 1); all 12 others are very similar. *M. fernholmi* has a shorter prebranchial length and a correspondingly longer trunk length and shorter tail. *Myxine debueni* also has somewhat shorter prebranchial and tail lengths, but the trunk length is similar to that of other species, except for *M. fernholmi*. The few specimens available (2 to 4) in 7 of the 14 species inhibits speculation as to relationships, geographical separation notwithstanding. Most counts are similar for most

[1] Fernhom, B. Swedish Museum of Natural History, Section for Vertebrate Zoology, P.O. Box 50007, 5-110405, Stockholm, Sweden. Personal commun., May 1994.

Table 1

Body proportions (mean and range in % of TL) for new world species of *Myxine*.

	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
No. of specimens examined	572	20	4	4	2	136	3	2	2	3	131	271	43	78	143
Size range (mm)	125–650	165–286	460–540	540–846	540–570	209–522	655–820	175–183	440–490	510–565	91–394	141–659	271–473	117–501	227–387
Prebranchial length	29	31	30	22	—	26	27	—	—	27	27	28	29	28	27
	29–30	27–34	29–32	20–25	24–25	25–28	27–28	24–26	28–29	27–28	26–32	26–31	26–31	23–30	24–30
Trunk length	57	51	59	70	—	61	61	—	—	61	58	59	59	58	58
	55–58	52–56	57–60	67–72	66–69	58–65	61–62	57–59	58–60	59–62	53–60	56–62	56–61	55–62	54–62
Tail length	13	15	12	9	—	11	12	—	—	13	15	13	13	11	15
	10–15	13–17	11–14	8–10	8–10	10–12	12–12	11–12	13–13	12–13	11–19	11–15	11–14	12–17	13–17
Body width	5	4	4	4	—	4	3	—	—	4	4	4	4	4	5
	4–6	3–5	3–5	3–5	4–5	3–5	2–4	4–4	4–4	4–4	2–5	3–5	4–6	2–5	3–6
Body depths															
Including ventral finfold	7	6	6	5	—	5	4	—	—	4	6	5	6	6	7
	6–8	5–9	5–7	4–7	5–6	4–6	4–4	4–6	6–6	4–5	4–8	4–7	4–8	4–7	5–9
Excluding ventral finfold	5	5	5	5	—	5	4	—	—	4	5	5	5	7	5
	4–7	4–7	4–6	4–6	5–6	4–5	4–4	3–6	4–5	4–4	5–7	3–7	4–7	3–7	5–8
Over cloaca	5	5	4	4	—	4	4	—	—	4	5	4	5	4	5
	3–5	4–7	4–5	3–5	4–4	3–5	3–4	4–4	3–5	4–4	4–6	4–5	4–6	3–5	4–6
Tail	5	6	5	4	—	4	4	—	—	4	5	5	5	4	5
	5–6	4–7	4–5	4–6	4–4	3–5	4–4	4–5	5–6	4–5	4–7	4–6	4–6	3–6	4–6

Table 2

Numbers of prebranchial slime pores for new world species of *Myxine*.

No. of prebranchial slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
18	1					2									
19	8					4									
20	26					3									1
21	58				2	24									1
22	76	1				45		1			3			1	2
23	90	3		2		39		1						2	6
24	75	5				35					2				15
25	56	5	1	1		23					3			1	17
26	25	4		1		13					4	1	1	8	16
27	14	2				7					9	6		10	25
28	10		1			5					14	13	3	6	13
29	1										10	29	5	10	15
30	2		1				1				7	35	7	10	13
31							2		1	1	12	39	10	7	8
32	2		1						1	1	5	30	8	9	8
33	1										6	39	6	6	1
34											7	22	1	7	
35											1	19	2	5	1
36											6	16		2	1
37											3	12		2	
38											2	8		1	
39											7	9			
40											1	5		1	
41											3	3			
42											1	2			
n=	445	20	4	4	2	200	3	2	2	2	106	288	43	88	143
$\bar{x}$=	23.24	24.70				23.23					31.25	36.62	31.00	29.88	28.85

Table 3

Numbers of trunk slime pores for new world species of *Myxine*.

No. of Trunk slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
43		1													
44															
45		1													
46		2													
47		4													
48	1	2													
49	2	1													
50	2	4													2
51	5	4									1				4
52	22							1			2			1	5
53	51	1						1			5				14
54	83										4			1	17
55	86										7			4	14
56	79										7			8	20
57	51					1					14	1		10	12
58	29					2					14			6	26
59	19		1			2					9	2		10	12
60	4		1			5					13	7	1	8	9
61	3		2			5				1	8	7	5	7	3
62	1					16					4	17	4	5	3
63						21					1	20	5	3	2
64						31					3	35	5	5	
65						34			2	1		56	7	4	
66						34					1	43	5	3	
67						17					2	30	6	6	
68						13	1				3	34	2	6	
69						10						21	1	1	
70						5	1					13	2		
71						1	1					4			
72						2									
73						2						2			
74												1			
75					1										
76					1										
77												1			
78															
79												1			
80				2											
81															
82															
83				1											
84															
85															
86															
87				1											
n=	438	20	4	4	2	201	3	2	2	2	98	295	43	88	143
$\bar{x}$=	55.20	48.50				65.14					58.46	65.75	64.65	60.74	56.29

Table 4

Numbers of tail pores for new world species of *Myxine*.

No. of Tail slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
7	7		1	1	2										
8	48			2		4		1			1			1	1
9	108	1	9	1		17		1			2	7	3	3	2
10	127	5	1			59					23	29	22		16
11	116	8	1			70			2	1	34	93	15	25	22
12	33	5				40	2				22	102	3	20	47
13	2					9	1			1	5	38		25	37
14		1				1					1	11		10	16
15															2
16														4	
n=	441	20	4	4	2	200	3	2	2	2	88	280	43	88	143
$\bar{x}$=	10.00	11.05				10.78					11.06	11.67	10.50	12.26	11.50

Table 5

Total numbers of slime pores for new world species of *Myxine*.

No. of Total slime pores	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
77		1													
78															
79		2													
80	3	1													
81	2	1													
82	14	1						1							
83	19	4													
84	25	1													
85	28							1							2
86	45	1									1				
87	56	4													1
88	52	1													2
89	44	1									1			1	2
90	39	1				2					2			2	9
91	38					2									8
92	18	1				2					2			2	9
93	15										1			1	9
94	21		1			17					3			4	11
95	5		1			12					3			2	10
96	10					14					4			7	11
97	3					20					7			5	6
98	1					26					6			3	14
99						17					11	2		8	9
100	3		1			16					4	1		6	7
101						27					3	4	3	3	9
102	1					12					6	6	5	3	10
103					1	6					3	8	1	8	5
104			1		1	5					2	5	3	3	5
105						7					4	8	8	6	1
106						2					8	10	3	2	
107						4					3	15	1	1	1
108						6			1	1	3	23	5	1	2
109						2			1		1	26		2	
110										1	4	22	8	4	
111						2	1				2	24	2	1	
112											1	22	2	3	
113				1								18	2	3	
114				1			1				1	31		2	
115				1									12	4	
116							1				1	10			
117												6		2	
118											1	5		2	
119												4			
120												5			
121				1								4			
122												3			
123												1			
124												4			
n=	442	20	4	4	2	200	3	2	2	2	88	279	43	91	143
$\bar{x}$=	89.69	84.46				100.40					102.00	111.50	106.83	103.50	96.54

Table 6

Numbers of anterior and posterior unicusps for new world species of *Myxine*.

	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
No. of anterior unicusps															
4						1		2			1				1
5						2					21			2	28
6		4		2		15	1			2	92			25	184
7	1	5		2	2	115	2		1		11	31		40	11
8	5	9				65			1	1		294	7	8	
9	122	2				2						180	55		
10	269											7	27		
11	106		1												
12	11		1												
13	2		2												
n=	516	20	4	4	2	200	3	2	2	3	125	512	89	75	224
$\bar{x}$=	10.00	7.50				6.50					5.50	8.50	9.00	6.50	5.50
No. of posterior unicusps															
5						3		1			1			1	2
6				1		28		1			26			10	66
7		3		3	2	135	3			1	90	4		38	151
8	39	4				34			2	1	8	297	4	26	5
9	283	7								1		203	49		
10	175	6										8	33		
11	18		1										1		
12	1		3												
n=	516	20	4	4	2	200	3	2	2	3	125	512	87	75	224
$\bar{x}$=	10.00	8.50				6.50					6.50	8.50	9.50	6.50	6.50

Table 7

Numbers of total cusps for new world species of *Myxine*.

	3-cusp multicusp on anterior set of cusps					2-cusp multicusp on both the anterior and posterior sets of cusps									
Total cusps	*M. circifrons*	*M. mccoskeri*	*M. robinsi*	*M. fernholmi*	*M. debueni*	*M. hubbsi*	*M. hubbsoides*	*M. pequenoi*	*M. dorsum*	*M. knappi*	*M. australis*	*M. affinis*	*M. mcmillanae*	*M. limosa*	*M. glutinosa*
26								1							
27															
28								1							
29											1				2
30											6			2	3
31											9			6	7
32						3					11			10	
33						3					19			5	12
34					1	19	1		1		56			24	63
35						18					11			17	3
36		1		2	1	54	3		3	1	12			29	1
37		1		1		46					4			14	1
38		1			1	25				1	2	11		19	1
39		2				14				1		10		5	
40		1				14						68		4	
41		2				3						46		1	
42		2				1						55	3	1	
43	4											25	4		
44	9	2										34	9		
45	14	3										5	10		
46	60	4										2	9		
47	60												6		
48	107	1											3		
49	77														
50	85														
51	49														
52	30														
53	6														
54	10														
55	4														
56	1		2												
57			1												
58			1												
n=	516	20	4	4	2	200	4	2	4	3	131	256	43	137	93
$\bar{x}$=	49.50	41.45				36.00					33.68	42.00	45.00	36.00	33.67

species; numbers of trunk and total slime pores differ more widely, but there is frequent overlap. The total numbers of cusps (Table 7) show the greatest differences between species. The height of VFF shows considerable intraspecific variation; for example, in *Myxine circifrons* it varies between 1 and 12 mm. Both the numbers of fused cusps and the number of gill pouches are constant with only rare or aberrant variation and are extremely useful in separating the 14 species into groups. Five species have a 3-cusp multicusp on the anterior set of cusps. Of these five, *M. circifrons, M. mccoskeri,* and *M. robinsi* have 5 gill pouches and *M. fernholmi* and *M. debueni* have 6; the only new world species with 7 gill pouches is *M. pequenoi.* The remaining eight species have 6 gill pouches and a 2-cusp multicusp in both anterior and posterior sets of cusps. An additional, possibly diagnostic character is that *Myxine mccoskeri* and *M. pequenoi* mature at much smaller sizes than do the other species, and are here regarded as dwarfed. Prior to the permanent Panamanian land bridge, *M. circifrons* of the tropical Pacific, and *M. mccoskeri* and *M. robinsi* of the southern Caribbean Sea, may have represented the same species. Only these three species have five gill pouches; they also have in common the 3-cusp multicusp on the anterior row, and the anterior portions of the heads of *M. circifrons* and *M. robinsi* are notably and consistently whiter than in any of the other species. *M. mccoskeri* may have independently developed a dwarfed condition as well as a unique color pattern of reverse countershading, fewer trunk pores, and anterior unicusps. Hermaphroditism occurs frequently in all the large collections except in *Myxine circifrons.* The fact that in such a large number of hagfishes examined, only one specimen was found with fully developed filaments suggests that eggs are extruded very soon after becoming fully mature, regardless of time of year. We have found no indications of sexual dimorphism in color, body proportions, TL, or slime pore counts.

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Material examined

Myxine circifrons

SIO67-118 (51), 38°00'N, 123°31'W, 732 m; SIO64-449 (38), 32°54'N, 117°38'W, 961 m; SIO59-257 (13), 32°35'N, 117°28'W, 1,208 m; SIO74-611 (65), San Diego Trough, 1,201 m; SIO66-7 (34), 32°32'N, 117°27'W, 1,190 m; SIO68-119 (34), 32°27'N, 117°27'W, 1,244 m; SIO69-227 (15), 31°35'N, 116°05'W, 1,202 m; SIO68-118 (110), 25°37'N, 109°43'W, 1,244 m; SIO68-59 (14), 23°07'N, 109°19'W, 1,281 m; SIO68-60 (6), 23°07'N, 109°11'W, 1,830 m; SIO68-119 (25), 25°36'N, 109°45'W, 1,491 m; SIO73-290 (4), 09°48'N, 85°42'W, 994 m; SIO73-293 (3), 09°23'N, 85°00'W, 1,107 m; SIO73-294 (17), 09°24'N, 85°06'W, 900 m; SIO69-148 (7), 02°02'S, 81°10'W, 1,000 m; SIO90-26 (1), 03°15'S, 80°53'W, 960 m; SIO90-27, (1), 03°15'S, 80°55'W, 960 m; SIO90-25, (2), 04°10'S, 81°27'W, 1,860 m; MCZ 49585 (1), 33°17'S, 77°05'W, 1,510 m. Twelve specimens from IMARPE, with incomplete data, taken between 08°S and 17°S, 71° and 81°W, between 800 and 1,500 m.

Myxine hubbsi

SIO92-127 (223), 32°40'N, 118°12'W, 1,830 m; SIO65-451 (19), 32°40'N, 118°12'W, 1,742 m; SIO65-452 (82), 32°38'N, 118°08'W, 2,009 m; SIO68-676 (16), 32°39'N, 118°11'W, 1,830 m; SIO71-116 (1), 28°52'N 115°50'W, 2,004 m; SIO68-60 (37), 23°08'N, 109°16'W, 1,830 m; SIO68-61 (2), 23°06'N, 109°13'W, 2,196 m; SIO73-293 (16), 09°24'N, 85°06'W, 1,107 m; SIO83-288 (1), 09°44'N, 85°00'W, 2,181 m; SIO73-293 (1), 09°24'N, 85°00'W, 1,102 m; SIO92-114 (11), 03°41'S, 81°36'W, 2,440 m; SIO92-115 (7), 08°26'S, 80°37'W, 1,930 m; SIO72-176 (8), 21°37'S, 70°55'W, 2,114 m; MCZ-44897 (2), 34°12'S, 72°76'W, 1,475 m. Examined, but not listed, are numerous collections of few specimens each from off southern California.

Myxine australis

SIO78-39 (8), 45°36'S, 74°11'W, 120 m; SIO78-40 (80), 50°30'S, 75°20'W, 80 m; SIO78-41 (2), 54°15'S, 70°58'W, 4 m; SIO78-43 (1), 55°03'S, 68°10'W, 30 m; SIO78-44 (3), 55°49'S, 67°30'W; SIO78-45 (2), 55°10'S, 65°30'W, 146 m; SIO78-49 (3), 54°46'S, 64°03'W, 23 m; SIO78-51 (18), 54°45'S, 64°10'W, 14 m; USNM 3939 (20), 42°29'S, 78°46'W; AMNH 4098 (2), 51°10'S, 69°30'W; FURG-? (4), 48°18'S, 65°06'W; the following collections lack stated depths but were taken in the area of the Straits of Magellan: MCZ 32518 (1); MCZ 8351 (6); MCZ 3836 (16); MCZ 3836 (16);

MCZ 8837 (22); MCZ 8839 (30); MCZ 8842 (10); MCZ 24972 (19); MCZ 35198 (1); USNM 103769 (1); USNM 117329 (1); USNM 153595 (1); USNM 267750 (1); AMNH 4098 (2); SU 22678 (1); IU 2124 (1); IU 4293 (1).

Myxine affinis

SIO78-39 (8), 45°36'S, 74°11'W, 120 m; SIO78-40 (39), Isla Madre de Dios, Chile, 80 m; SIO78-41 (62), 54°14'S, 70°06'W, 4 m; SIO78-42 (7), 54°52'S, 70°58'W, 60 m; SIO78-43 (21), 55°03'S, 68°10'W, 30 m; SIO 78-44 (15), 54°45'S, 64°09'W; SIO78-45 (4) Bahia Windhond, Chile, 146 m; SIO78-50 (3), 54°54'S, 64°10'W, 14 m; SIO78-51 (31), 54°45'S, 64°10'W, 14 m; SIO83-121 (2), 54°22'S, 71°22'W. The following collections lack stated depths and coordinates but were taken in the area of the Straits of Magellan: MCZ 35198 (12); MCZ 8836 (3); MCZ 8837 (7); MCZ 8839 (1); MCZ 8840 (6); MCZ 8841 (11); MCZ 24972 (1); USNM 77377 (1);USNM 26715 (1); USNM 39039 (2); USNM 39140 (1); USNM 17418 (1); FMNH 9820 (3); SU 22678 (1).

Myxine limosa

SIO74-181 (28), 36°43.2'N, 74°38'W, 300 m; SIO74-185 (3), 37°05'N, 74°39'W, 280-360 m; SIO74-187 (4), 36°36'N, 79°42'W, 316 m; SIO74-188 (1), 38°18'N, 73°35'W, 215-250 m; SIO74-189 (4), 37°27'N, 74°30'W, 120-320 m; SIO74-190 (5), 36°19'N, 74°47'W, 310-400 m; SIO75-677 (5), 41°54'N, 69°50'W, 75 m; SIO75-678 (1), 41°53'N, 68°07'W, 183 m; SIO75-679 (2), 49°09'N, 66°56'W; SIO75-680 (5), 42°30'N, 66°04'W; SIO75-681 (3), 43°02'N, 64°32'W; SIO75-682 (1), 42°33'N,66°58'W, 293 m; SIO75-683 (6), 42°26'N, 68°44'W; SIO75-684 (1), 42°30'N, 69°20'W; SIO75-685 (2), 42°31'N, 69°42'W, 275 m; SIO75-686 (4), 42°33'N, 69°48'W, 275 m; SIO75-689 (3), 37°05'N, 74°40'W, 280-360 m; SIO77-101 (1), 39°35'N, 72°04'W, 201 m; SIO77-102 (1), 39°32'N, 72°22'W, 375-512 m; SIO77-103 (1), 41°32'N, 68°29'W, 86 m; SIO77-104 (1), 41°51'N, 68°05'W, 88 m; SIO77-105 (3), 39°12'N, 72°29'W, 302 m; SIO77-106 (1), 39°05'N, 72°43'W, 234 m; SIO77-107 (4), 38°30'N, 73°19'W, 220 m; SIO77-108 (1), 37°28'N, 74°24'W, 191 m; SIO77-119 (2), 37°54'N, 74°00'W, 261 m; ISH6-1965 (1), 45°06'N, 54°46'W; ISH42-1970 (1), 40°25'N, 68°10'W, 220-230 m; ISH-1987 (3), 66°38.6'N, 56°38.2'W, 540 m; ISH-7238-1982 (2), 66°04'N, 56°13.9'W, 323 m; ISH63-1987 (1), 63°05'N, 52°13'W, 127-155 m; ISH431-1986 (1), 57°38'N, 18°13'W, 1,006 m; ISH5-1965 (1), 45°06'N, 54°48'W, 180-260 m; ISH2-1970 (1), 45°00'N, 54°47'W, 175 m; ISH23-1961 (33), 44°19'N, 54°27'W, 175 m; ISH42-1970 (1), 40°25'N, 68°10'W, 230 m; ISH3653-1979 (1), 33°45.8'N, 76°05.6'W, 608 m.

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Covariation between growth and morphology suggests alternative size limits for the blacklip abalone, *Haliotis rubra*, in New South Wales, Australia

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Abstract.—Growth of the blacklip abalone, *Haliotis rubra*, was estimated from 1,464 individuals that were tagged and left at large for up to five years at seven sites in New South Wales, Australia. Both the shape of the fitted growth curves and the average growth rates differed significantly among sites, separated by only 1–20 km. There was also significant variation in the growth of individual abalone within sites and this variation differed among sites. Abalone at sites where they grew quickly reached larger lengths and were morphologically different from those at sites where they grew slowly. For example, the shells of abalone from sites where they grew slowly were wider and heavier at a given length than those from sites where they grew quickly. The implication that rates of growth in width are less variable than growth in length suggests that a minimum legal width limit may be more appropriate than the present size limit that is based on length. A minimum legal width limit would redistribute fishing effort away from sites where abalone grow in length quickly towards sites where they grow slowly, including sites which are presently unfished because few individuals reach the minimum legal length. If this were possible, it would reduce the differences in exploitation among sites which, at present, have the potential to seriously deplete populations at sites where individuals grow quickly.

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Legal restrictions on the minimum size of individuals allowed to be harvested are used to manage many fisheries. The theory behind their use asserts that by delaying the harvest of individuals until they have grown to a certain size, both yield and egg production can be increased (Beverton and Holt, 1957). Appropriate minimum size limits have traditionally been estimated by considering average rates of growth, mortality, and reproduction (Goodyear, 1993). Spatial variation in demography can complicate the use of a single size limit for a stock by making different size limits appropriate in different areas. Enforcement of different size limits over large spatial scales is possible (e.g. Guzmán del Próo, 1992), but if demography varies over small distances, appropriate size limits are difficult to enforce.

A common finding of studies on the growth of abalone has been that individuals at different sites can grow at markedly different rates (Sainsbury, 1982; Breen, 1986; Tegner et al., 1989). Despite this, there have been few systematic attempts to determine the spatial scale over which differences in growth occur (see Day and Fleming, 1992, for a review). Nonetheless, it is apparent that growth can vary among regions separated by hundreds of kilometers (Nash, 1992) and among sites separated by tens of kilometers (Breen, 1986). As well as differing in their rate of growth, abalone that grow quickly will, in general, reach larger sizes than abalone that grow slowly (e.g. McShane, 1992; Nash, 1992). Consequently, many abalone fisheries contain populations with individuals that grow very slowly to only small sizes (Sloan and Breen, 1988; Tegner et al., 1989; Nash, 1992). Because minimum legal sizes are, in general, enforced over areas larger than those over which such variation in growth can occur, these sites often remain unfished.

Commercial fishing of abalone *Haliotis rubra* in New South Wales (NSW), Australia began in the early 1960's. Initially, divers harvested abalone of any size, but in 1973 a minimum legal length limit of 100 mm was introduced. This length limit was chosen to ensure that abalone recruiting to the fishery had reproduced at least once after reaching sexual maturity at approximately 80–90 mm. As fishing pressure increased through the 1970's and 1980's, it became apparent that the length limit of 100 mm

was not conserving enough egg production (Hamer, 1983). In response, the minimum legal length limit was increased in a series of increments from 100 mm in 1979 to 115 mm in 1987. An unfortunate consequence of these increases was the concentration of fishing effort at sites where abalone grew quickly and to large sizes (see also McShane, 1992). Because of this high level of effort and the limited dispersal of larval abalone (Prince et al., 1987), such sites were often overexploited, whereas in other areas where abalone grew more slowly to smaller sizes the populations were underexploited.

In this study, we describe a tagging study of variation in the growth of *Haliotis rubra* at seven sites along the NSW coast. These sites were grouped into four locations encompassing most of the geographical range of the fishery. This provides an indication of the variability in growth of the species at three spatial scales: among locations separated by hundreds of km, among sites separated by 1–20 km, and among individual abalone within the sites. In addition we describe morphological differences among the abalone that appear to be related to their rate of growth. This link between growth and morphology suggests that a minimum legal width limit may be more appropriate than the present size limit based on length.

Materials and methods

Sites and tags used

Abalone were tagged at seven sites, spanning almost 1,000 km of coastline, that were chosen because they were commonly used by commercial divers in the NSW abalone fishery (Fig. 1). Six of the sites were grouped into three locations (Broughton Island, Sydney, and Eden) each with two sites (referred to as I and II) separated by between 1 and 20 km. The single site at Merrys Beach was approximately midway between those at Sydney and Eden (Fig. 1). Supplementary tagging was also done at Bittangabee Bay near Eden (Fig. 1). This site was not commonly used by commercial fishermen because few individuals reached lengths above the 115-mm minimum legal limit. Estimates of growth parameters for Bittangabee Bay were not calculated separately because only 20 individuals were recaptured. These abalone were, however, used in the estimation of a growth curve for all recaptured individuals and in the relationship among morphological variables (see below).

Small (≈2 × 10 mm), numbered plastic tags were attached to abalone with a cyano-acrylate glue between 20 May 1975 and 3 October 1981. This procedure required that abalone be removed from the water and their shells dried with compressed air before tagging. Individuals were chosen to make the size range at tagging representative of the population at each site. The maximum diameter (i.e. length) of each shell was measured to the nearest 0.5 mm, and the abalone were then replaced in the area near where they were collected. Samples of these tagged abalone were recaptured at opportunistic times between 11 December 1975 and 18 May 1982.

Patterns in growth

Estimates of growth were obtained by using procedures based on a mark-recapture analogue of Schnute's (1981) general growth model (see Francis, in press). Schnute's model relates size to age by several parameters, including two (a and b) which combine to describe a range of traditional growth curves including the von Bertalanffy ($a > 0, b = 1$), Richards

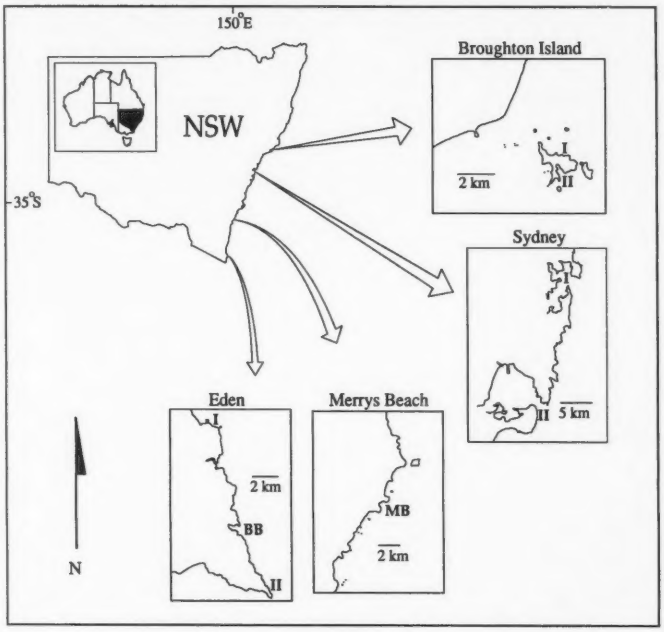

Figure 1

Map of Australia (inset) and New South Wales (NSW), showing the position of eight sites within four locations where blacklip abalone, *Haliotis rubra*, were tagged. Sites I and II within each location are as indicated on the maps; BB = Bittangabee Bay, MB = Merrys Beach.

($a > 0$, $b < 0$), logistic ($a > 0$, $b = -1$), and Gompertz ($a > 0$, $b = 0$) models (Schnute, 1981). Francis (in press) reparameterized this model to express observed increments in length during tagging (ΔY) as a function of the observed length at tagging (Y_t) and time at liberty (Δt). The model can be reparameterized further, so that growth can be described in terms of average annual growth for individuals of a given size (see Francis, 1988a). The general model where both $a \neq 0$ and $b \neq 0$, was

$$\Delta Y = -Y_t + \left[Y_t^b e^{-a\Delta t} + c(1-e^{-a\Delta t})\right]^{\frac{1}{b}},$$

where $$a = \ln\left[\frac{y_2^b - y_1^b}{\lambda_2^b - \lambda_1^b}\right],$$

$$c = \frac{y_2^b \lambda_1^b - y_1^b \lambda_2^b}{\lambda_1^b - y_1^b + y_2^b - \lambda_2^b}, \text{ and}$$

$$\lambda_1 = y_1 + g_1 \text{ and } \lambda_2 = y_2 + g_2.$$

The model was fitted to the observed increments by using maximum likelihood (Francis, 1988b). Parameters estimated during this process include the mean annual growth rates (g_1 and g_2) at two sizes (y_1 and y_2) and the parameter b. These parameters together combine to define the parameter a, and hence the shape of the fitted growth curve.

Several other parameters were also considered, and were included in the model if they significantly improved the fit (see Francis, 1988b). Two parameters describing seasonal variation in growth were examined by replacing Δt above with $\Delta t + (\phi_{t_r} - \phi_{t_t})$ where for any time (t_i)

$$\phi_{t_i} = \frac{u\left(\sin(2\pi[t_i - w])\right)}{2\pi}$$

and t_t and t_r are the times at tagging and recapture. The parameters u and w then describe the amplitude and phase of seasonality in growth, respectively. A parameter describing variation in growth among individuals was also examined, where the mean (μ_g) and standard deviation (σ_g) of the expected increment in length were related by

$$\sigma_g = v\mu_g,$$

where v is the coefficient of variation in growth. A parameter describing contamination by outliers was also examined, but it never added significantly to the model (see Francis 1988b).

The error model used considered errors due to variation in growth and measurement by

$$\Delta Y_{obs} = \Delta Y \varepsilon_g + \varepsilon_m,$$

where the observed increment in length (ΔY_{obs}) was a function of that predicted by the growth model (ΔY) and errors due to variation in growth (ε_g) and measurement (ε_m), assuming $\varepsilon_g \sim N(1, \sigma_g)$ and $\varepsilon_m \sim N(\mu_m, \sigma_m)$. As such, μ_m represents measurement bias (i.e. consistent difference in measurement between marking and recapture) and σ_m represents random error in measurement. Since better estimates of the growth parameters can be achieved when both μ_m and σ_m are known (Francis, in press), they were estimated by repeatedly measuring the same set of shells (n=50) after the tagging program had finished. Measurement bias was disregarded (μ_m=0) because the same people used identical techniques to measure abalone at tagging and recapture. Random errors in measurement among replicate readings and among readers were similar in size, and as a consequence σ_m was set to 0.65 for all analyses. Following fitting of the model, plots of residuals against length at tagging and time at liberty were investigated for any systematic lack of fit.

The parameters y_1 and y_2 should be chosen to span the lengths at tagging and to enable reliable estimates of g_1 and g_2 (Francis, 1988b). Because of differences in the length of abalone tagged among the sites, appropriate sizes for y_1 and y_2 also differed among sites. To facilitate comparison, y_1 and y_2 for each site were chosen from three standard lengths: 65, 90, and 115 mm. At sites where few small abalone were tagged, annual growth rates were estimated at 90 and 115 mm. Alternatively, at sites where few large abalone were tagged, annual growth rates were estimated at 65 and 90 mm. Once fitting of the model was completed, the annual growth rate at the third standard length was also calculated. This growth rate is defined by the parameters chosen during fitting of the model. Comparisons among estimated parameters were made by using t-tests.

To facilitate the comparison of our estimates of growth with those previously published, we also fitted the traditional von Bertalanffy growth model. This was done within the framework described above (see Francis, 1988b). To further aid the comparison of growth rates among studies, we converted the traditional von Bertalanffy parameters estimated from tagging data (k and L_∞) to parameters describing estimates of annual growth at the standard sizes used in this study. This was also done for previously pub-

lished estimates of growth derived from tagging studies in which similar tagging methods were used.

Relation of growth to morphology

The shells of 390 recaptured abalone were retained for further measurement. This allowed us to relate present morphology of the shells to past growth rates. Few shells were retained from Broughton Island I or Eden I because the abalone were used in separate experiments to estimate fishing mortality. Measurements taken included the maximum and minimum diameters (length and width), the width of the ventral ridge of the shell at the aboral margin (ridge), and the dry weight of the shell. Relationships among these variables were investigated by correlation. To relate present morphology to past growth, the length of all shells was related to their width, weight (log transformed), and ridge by using multiple linear regression. The residuals from this relationship then indicate whether a shell is longer or shorter than expected given the other morphological variables. In a similar way, all the tagging data were combined into one growth model. The residuals from this growth model then indicate whether an abalone has grown faster or slower than expected. By averaging the residuals from the morphological relationship and the growth curve across all individuals at a site, any relationship between rates of growth and shell morphology among sites should be apparent.

Results

A total of 1,464 abalone were recovered from the seven sites. At tagging, these individuals ranged in size from 15 to 152 mm, with a mean size of 91.1 mm (SE=0.7). The size of recaptured abalone at tagging differed among sites. Few of the individuals recaptured at Broughton Island II and Eden I were small when tagged (Fig. 2A). In contrast, few large abalone were recaptured from Merrys Beach, both sites in Sydney, and from Eden II.

Tagged abalone were at large for a period between 8 and 1,736 days, although most (98%) of the individuals were recaptured within two years of release. The range of times between tagging and recapture of abalone differed among sites (Fig. 2B). There were generally shorter times between tagging and recapture in Broughton Island I and Sydney I, and longer times at Merrys Beach (Fig. 2B). During the tagging period increments in size ranged from –8 mm to 84 mm, with an average of 11.8 mm (SE=0.4). Negative growth may have been caused by erosion of the shell.

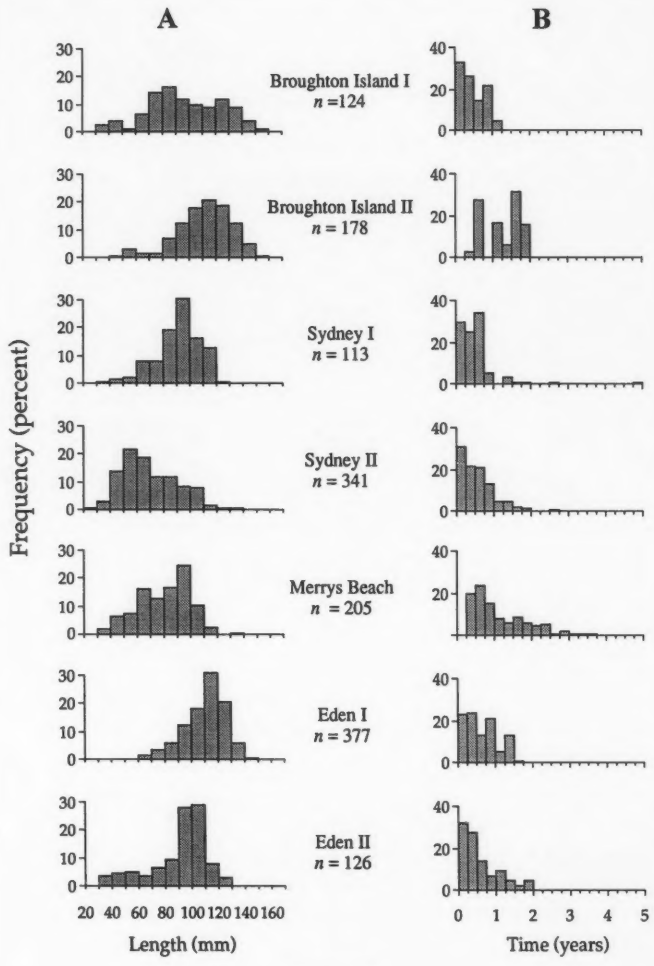

Figure 2

Distribution of (**A**) length at marking (Y_t) and (**B**) time at liberty (Δt) for recaptured blacklip abalone, *Haliotis rubra*, at seven sites.

Patterns in growth

The shape of the fitted growth curve differed significantly among sites (t-tests, $P<0.05$; Table 1). At Broughton Island I and Sydney I, the fitted growth curve was similar to a traditional von Bertalanffy shape ($a > 0$, $b \approx 1$ in Table 1), whereas at Eden II it was more similar to a Gompertz shape ($a > 0$, $b \approx 0$ in Table 1), and at Merrys Beach more similar to a logistic shape ($a > 0$, $b \approx -1$ in Table 1). All curves were asymptotic and expected growth approached zero (Fig. 3B). The size at which expected growth equalled zero differed among sites and ranged from 118 mm at Merrys Beach to 151 mm at Broughton Island II (Fig. 3B; Table 1).

Estimates of average annual growth rates differed significantly among the seven sites (Table 1). Abalone at the two sites on Broughton Island had faster rates of growth than all other sites. At Broughton Island II a 65-mm abalone was expected to grow to the 115-mm length limit in approximately 18 months (Fig. 3A). Above 115 mm, growth declined rapidly so that in the next year expected growth was less than 10 mm. The rate of decline in growth rate then slowed, and growth was expected to continue until 151 mm (Fig. 3; Table 1). In contrast, growth at Sydney I was much slower; a 65-mm individual was expected to take almost 9 years to grow to 115 mm (Fig. 3A). Growth rate declined at an approximately constant rate throughout life (i.e. approximating a von Bertalanffy growth curve) until individuals were expected to have no growth at 126 mm (Fig. 3; Table 1). At Merrys Beach, abalone were expected to grow from 65 mm to 90 mm within a year, but then growth declined rapidly and individuals were expected to grow only just above the minimum length limit of 115 mm (Fig. 3A). Growth rates at Sydney II and Eden II were not significantly different at any of the standard sizes (Table 1).

There was significant variation in growth among individual abalone within all sites (Table 1). Variation in growth among abalone at Merrys Beach was significantly less than that at all other sites and significantly greater at Broughton Island II, Sydney I, and Eden I (t-tests, $P<0.05$). The standard deviation of the observed growth increment ranged from 0.29 times the expected increment at Merrys Beach to 0.87 times the expected increment at Eden I (Table 1). This range implies that two-thirds of the abalone at Merrys Beach will grow between 0.71 and 1.29 times the expected increment, whereas at Eden I, two-thirds of the abalone will grow between 0.13 and 1.87 times the expected increment (Fig. 4).

Parameters representing seasonal variation in rates of growth significantly improved the fit of the model at three of the seven sites (Table 1). At Broughton Island II, peak growth rates occurred during late October at 1.9 times the minimum growth rate in late April. In contrast, peak growth rates at both Sydney II and Eden I occurred in December at a rate 2.0 and 2.9 times the minimum, respectively

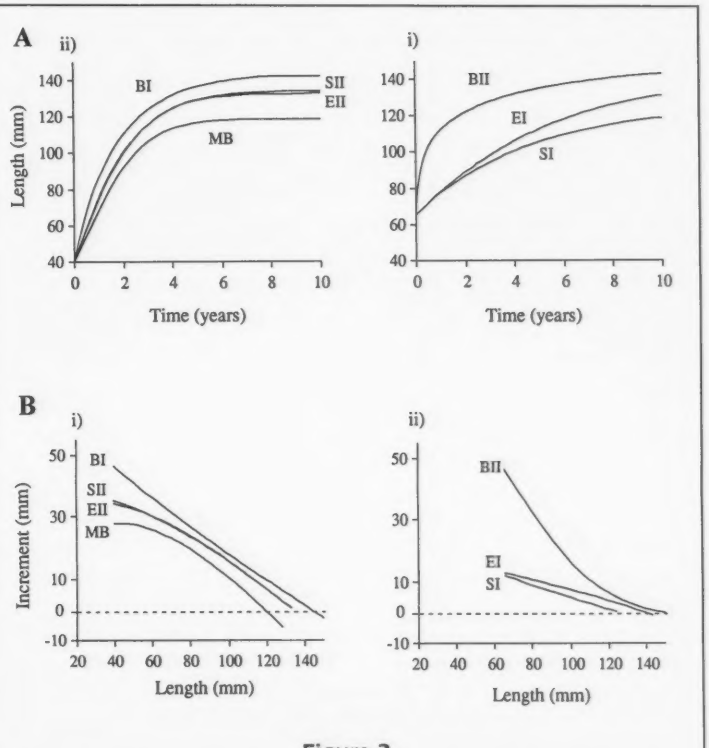

Figure 3

Predicted mean growth of blacklip abalone, *Haliotis rubra*; (**A**) over 10 years for individuals of a given size and (**B**) over 1 year for individuals of a range of sizes. Growth is shown from (i) 40 mm at sites where many small abalone were tagged and (ii) 65 mm at sites where few small abalone were tagged up to the size of the largest abalone. Sites are abbreviated as follows: BI and BII = Broughton Island I and II; SI and SII = Sydney I and II; MB = Merrys Beach; EI and EII = Eden I and II.

Table 1

Estimates of growth parameters and their standard errors (in brackets) for blacklip abalone, *Haliotis rubra*, from tag returns at seven sites. Parameters estimated during fitting are shown in light type; those defined by the fitted parameters are shown in bold. Expected annual growth rate at 65, 90, and 115 mm is shown as g_{65}, g_{90} and g_{115}, respectively. See Materials and Methods section for a description of other parameters. Blanks occur where parameters did not add significantly to the fitted model.

	Site						
	Broughton Island		Sydney			Eden	
Parameter	I	II	I	II	Merrys Beach	I	II
Curve shape parameters							
b	1.33 (0.30)	7.58 (1.13)	1.33 (0.41)	0.25 (0.09)	–0.74 (0.12)	0.50 (0.37)	0.04 (0.10)
a	**0.59 (0.13)**	**0.11 (0.05)**	**0.20 (0.06)**	**0.66 (0.08)**	**0.89 (0.08)**	**0.22 (0.04)**	**0.71 (0.14)**
Growth rate parameters							
g_{65} (mm·year^{-1})	**33.68 (1.52)**	46.93 (2.78)	12.25 (0.77)	28.66 (0.78)	24.63 (0.60)	**12.71 (0.92)**	28.80 (0.96)
g_{90} (mm·year^{-1})	22.24 (0.95)	24.11 (1.39)	6.91 (0.52)	19.58 (0.67)	15.22 (0.34)	9.14 (0.49)	19.87 (0.69)
g_{115} (mm·year^{-1})	11.52 (0.62)	8.36 (0.62)	**2.06 (0.91)**	**8.87 (0.77)**	**2.21 (0.42)**	4.86 (0.28)	**8.85 (1.40)**
Seasonal parameters							
u (year)		0.31 (0.08)		0.48 (0.05)		0.33 (0.07)	
w (year)		–0.19 (0.01)		0.00 (0.01)		–0.01 (0.03)	
Growth variability parameter							
v	0.54 (0.04)	0.73 (0.05)	0.76 (0.06)	0.48 (0.02)	0.29 (0.01)	0.87 (0.05)	0.39 (0.02)
Asymptote (mm)	143	151	126	133	118	140	133
Largest abalone (mm)	151	152	124	132	130	143	129
n	124	178	113	341	205	377	126

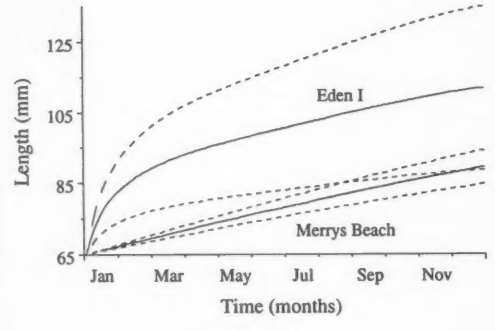

Figure 4

Predicted mean growth (solid line) and 50% confidence intervals (dashed line) of 65-mm blacklip abalone, *Haliotis rubra*, over one calender year at two sites.

(Fig. 4). At Broughton Island I, Sydney I, Merrys Beach, and Eden II there was no evidence of any significant seasonal variation in growth rates (Table 1).

Relation of growth to morphology

There were differences in the morphology of abalone among sites. For example, the shells of abalone recaptured from Merrys Beach were, on average, wider, heavier, and had a larger ridge than individuals of the same length from Sydney II (Fig. 5). There was a significant difference among sites in the slope of each of the relationships (t-tests, $P<0.05$), suggesting that the difference in morphology of individuals among sites changed with length. The shell of a 100-mm abalone from Merrys Beach was, on average, approximately 5 mm wider, 8.3 g heavier, and had a 1.7 mm larger ridge than the shell of a 100-mm abalone from Sydney II (Fig. 5). Differences in the width and ridge of shells among the sites increased with length, whereas differences in the weight of shells decreased with length (Fig. 5). The width, weight, and ridge of all shells were each significantly correlated with the other variables (width vs. weight r=0.76; width vs. ridge r=0.58; weight vs. ridge r=0.68; n=390 for all correlations).

Abalone from sites where their average growth was faster were morphologically different from those

where their average growth was slower (Fig. 6). The residuals of the general growth model were significantly higher at sites such as those at Broughton Island, Sydney II, and Eden II than at Eden I, which was, in turn, significantly higher than Merrys Beach and Sydney I, or Bittangabee Bay (t-tests, $P<0.05$; Fig. 6). This ranking corresponds closely with the estimates of average growth rates in Table 1. The residuals of the relation between length and the independent variables width, weight, and ridge were generally higher at sites where growth was also high (Fig. 6). That is, given their width, weight, and ridge, abalone at sites where they grew quickly were longer than those where they grew slowly. Alternatively, shells of abalone of a given length at sites where they grew quickly were thinner, lighter, and had a smaller ridge than those at sites where they grew slowly.

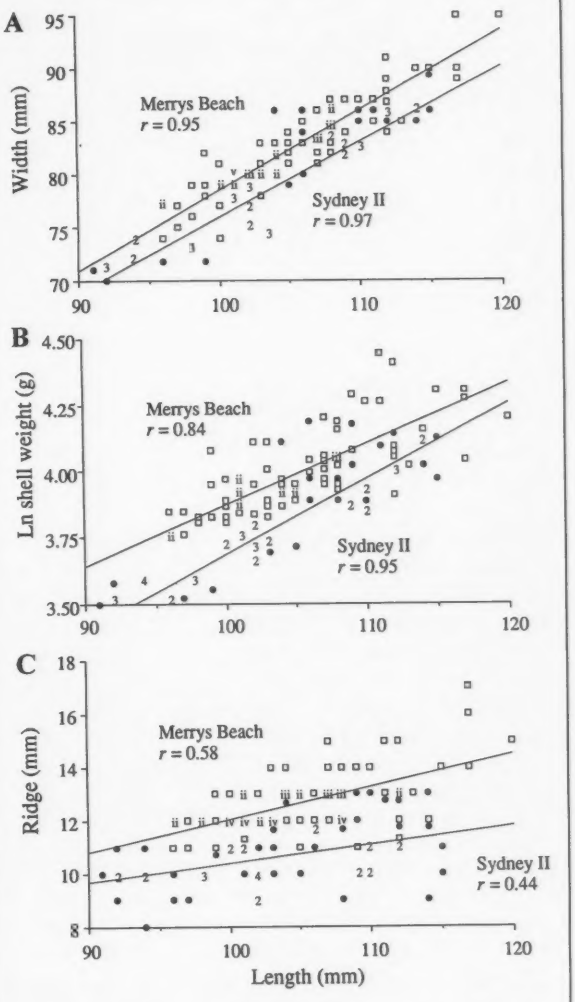

Figure 5

Relationshjp between shell length and (**A**) shell width, (**B**) shell weight, and (**C**) shell ridge for blacklip abalone, *Haliotis rubra*, recaptured from two sites. Filled circles and arabic numerals denote abalone from Sydney II, and open squares and roman numerals denote abalone from Merrys Beach. Numerals denote the number of coincident points, and the lines were fitted by least-squares.

Discussion

Patterns in growth

The intense spatial variation in growth that we observed for *Haliotis rubra* in NSW appears to be characteristic of abalone populations worldwide (Day and Fleming, 1992). At the smallest spatial scale, there was significant variation in the growth rate of abalone within sites. At a larger scale, both average rates of growth and the magnitude of within-site variation differed among sites separated by only 1–20 km. Perhaps the most likely explanation for variation in growth over these smaller spatial scales involves variation in the supply of food, related to local habitat and hydrographic conditions (Day and Fleming, 1992). At the largest spatial scale, average growth rates at the two sites on Broughton Island were significantly higher than all others. Broughton Island is approximately 300 km farther north than any of the other sites, and abalone around the island are likely to be exposed to higher water temperatures than abalone farther south. Water temperature is known to affect the growth rate of abalone (Day and Fleming, 1992), but the trend in NSW stands in contrast to that found for *H. rubra* in Tasmania, where abalone grow more slowly in the warmer, northern areas (Nash, 1992).

Several previous studies have found a relation between the rate of growth and maximum size of abalone at a site (Shepherd and Hearn, 1983; McShane et al., 1988; Sloan and Breen, 1988; Nash, 1992). In general, abalone at sites where they grow quickly reach larger sizes than those at sites where they grow slowly. A similar situation appears to exist in NSW where abalone from the two sites on Broughton Island had the fastest average growth rates and reached the largest shell lengths (i.e. >150 mm, Table 1). In comparison, the slowest average growth rates

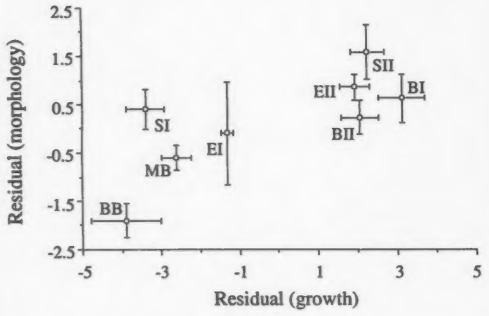

Figure 6

Average residual from growth and morphological relationships for blacklip abalone, *Haliotis rubra*, recaptured from eight sites. Vertical and horizontal bars are standard errors. Sites are abbrieviated as follows: BI and BII = Broughton Island I and II; SI and SII = Sydney I and II; MB = Merrys Beach; EI and EII = Eden I and II; BB = Bittangabee Bay.

were recorded at Sydney I where the largest abalone was smaller than those at all other sites (i.e. 124 mm, Table 1). Despite this general relationship, slow rates of growth were recorded at Eden I, but growth was expected to continue until 140 mm, and many abalone were found over 130 mm in length.

Direct comparison of growth rates estimated by different studies are complicated by the variety of methods used for tagging and analysis. For example, tags attached by wire through an abalone's respiratory pore can affect growth (McShane et al., 1988), and growth parameters estimated from tagging and age-length data need to be interpreted differently (Francis, 1988a). Any comparison of growth rates among studies can also be confounded by the growth model used to fit the observed increments (e.g. compare estimates of growth from the different models used in Tables 1 and 2). When fitted with a similar growth model to past studies, our estimates of the growth of abalone in NSW span almost the entire range of those from similar studies in other states of Australia (Table 2). In addition, estimates of growth at the two sites on Broughton Island are consistently higher than any previously reported natural growth rates for the species.

Relation of growth to morphology

Differences in the morphology of individuals among populations have been reported for a range of gastropod species including abalone (see review by Vermeij, 1980). Despite the significance of variation in the morphology of *Haliotis rubra* in NSW, differences among sites were not large (e.g. compare with those of Breen and Adkins, 1982). There was also substantial variation in the morphology of individuals within sites. Despite little evidence, explanations for the variation in morphology of abalone usually concentrate on environmental rather than on genetic factors (McShane et al., 1988). As for other gastropods, it is likely that all aspects of shell growth that result in morphological differences are influenced by a variety of factors including exposure to wave action, diet, and water temperature (Tissot, 1992; Belda et al., 1993). Although we only present evidence to suggest that differences in morphology of the shell exist among populations of *Haliotis rubra*, there is also evidence for related morphological variation in the soft tissues (McShane et al., 1988).

Differences in the morphology of *Haliotis rubra* among sites were related to differences in growth. At sites where they grew slowly, the shells of abalone were wider, heavier, and had a broader ridge than those at sites where they grew quickly. These observations are similar to those made on other species of abalone (e.g. Breen and Adkins, 1982; Shepherd and Hearn, 1983; Tissot, 1988) and perhaps are not surprising considering that the processes proposed to influence both growth and morphology are similar. Inclusion of the slow-growing population at Bittangabee Bay strengthened the relation between growth and morphology that was evident among the seven sites where extensive tagging was done. Extensive tagging was not done at Bittangabee Bay because few animals grow above the present 115-mm legal length limit and hence the site is rarely fished by commercial divers. Because of the relationship between the maximum size reached by abalone at a site and their growth rate, very slow growing sites are rarely visited by commercial divers and, consequently, were not chosen for tagging in this study. As a result, our estimates of growth represent the higher end of the range of growth rates for abalone in NSW.

The increased width and weight of shells from abalone that grew slowly in length imply that rates of shell growth in width and weight are more consistent among sites than growth in length. This might be explained by increased synthesis of the organic matrix of the shell when energy is plentiful (Palmer, 1992) and can be devoted to expansion of the mantle at the growing edge and hence to rapid growth in length (Belda et al., 1993). Alternatively, when less energy is available, reduced synthesis of the organic matrix may result in a slower expansion of the growing edge of the mantle, causing slower growth in length and proportionally more growth in width and weight (Vermeij, 1980). Such an explanation would

not require any variation in the rate of incorporation of calcium-carbonate, which may continue regardless of the rate of synthesis of the organic matrix (see similar arguments for fish otoliths in Gauldie and Radtke, 1990). Because calcium-carbonate dominates a shell by weight (Palmer, 1992), if the rate of incorporation of calcium-carbonate was similar among different populations, the total weight of the shell might be a reliable indicator of the age of the abalone (see the literature on use of the weight of otoliths to age fish, e.g. Worthington et al., in press). The ability to age abalone is obviously desirable, but much doubt exists about present techniques of ageing, particularly for *Haliotis rubra* (McShane and Smith, 1992). This uncertainty emphasizes the need to investigate alternative methods to age abalone, one of which may be shell weight (Worthington et al., unpubl. data).

Table 2

Comparison of estimates of growth for blacklip abalone, *Haliotis rubra*. Note the estimated growth of abalone below 80 mm from Prince et al. (1988) was determined by analysis of size-frequency distributions; all other estimates were derived from tags glued to the external surface of the shell. Expected annual growth rate at 65, 90, and 115 mm is shown as g_{65}, g_{90}, and g_{115}, respectively.

Study and location	g_{65}	g_{90}	g_{115}	L_∞	k
	(mm·year^{-1})			(mm)	(year^{-1})
Shepherd and Hearn, 1983					
South Australia	21.3	14.1	6.9	139	0.34
	21.3	14.4	7.6	143	0.32
	26.4	18.0	9.7	144	0.41
McShane et al., 1988					
Victoria	13.1	6.8	0.5	117	0.29
	16.5	9.2	1.8	121	0.35
	16.1	10.2	4.3	133	0.27
Prince et al., 1988					
Tasmania	21.0	12.6	6.3	140	0.29
McShane and Smith, 1992					
Victoria	26.9	19.2	11.5	152	0.37
	16.5	9.2	1.8	121	0.35
	7.8	4.3	0.8	121	0.15
This study, NSW					
Broughton Island					
I	38.0	25.7	13.3	142	0.68
II	28.0	19.8	11.5	150	0.40
Sydney					
I	16.3	9.3	2.3	123	0.33
II	32.1	21.1	10.1	138	0.58
Merrys Beach	22.6	11.7	0.9	117	0.57
Eden					
I	18.0	12.1	6.2	141	0.27
II	30.4	17.9	5.5	126	0.69

Potential for alternative size limits

The present 115-mm minimum legal length limit is enforced along the entire coast of NSW for both the commercial and recreational fisheries. This size limit was chosen by considering average rates of growth, mortality, and reproduction in an attempt to maximize yield from the entire stock. The intense spatial variation in growth that we have described creates several problems which combine to restrict the effectiveness of the length limit. For example, because the 115-mm length limit was chosen by considering average rates of growth, it is less appropriate for sites where abalone grow faster or slower than average. At sites where they grow quickly, abalone rapidly reach the minimum legal length and may be harvested before contributing significantly to levels of egg production. Because of the limited dispersal of larval abalone (Prince et al., 1987), such sites have a limited capability to recover after fishing and hence may easily become overexploited. In contrast, at sites where they grow slowly, abalone take a longer time to reach the minimum legal length limit, and few are removed by divers. Consequently, rates of egg production may be high but they do not contribute significantly to other populations because of the restricted dispersal of larvae (see also Tegner, 1993). In addition, because of the link between growth rate and the maximum length of abalone at a site, as the maximum length of abalone at the site is below the minimum length limit, many populations can never be fished. Different length limits related to the growth of abalone at a site would be desirable, but considering the small spatial scales over which significant differences in growth can occur, their enforcement would be impractical.

An alternative approach to applying different length limits would be to enforce a size limit based on shell width. Because of the differences in morphology of abalone among sites with different growth rates, a width limit would allow individuals from sites where they grow slowly to be removed at shorter lengths than those where they grow quickly. This

would have two potentially desirable consequences. First, it would distribute effort more evenly across sites with the entire range of growth rates. This would occur because more abalone could be collected from sites where they grow slowly, and less would be available at sites where they grow quickly. Following the progressive increase in length limit during the 1980's, most fishing became concentrated at sites where abalone grew quickly (see also McShane, 1992). As described above, the length limit at these sites was also lower than appropriate, which in combination with the intense fishing effort, so that populations at sites where growth was fast were exploited at considerably higher rates than those for other populations.

The second desirable consequence of enforcing a width limit would be to allow the collection of abalone from sites that are presently unfished because abalone grow very slowly and few reach the minimum legal length (i.e. as stunted abalone). If an appropriate width could be chosen, more abalone would be available for collection at sites where they grow slowly, making it viable for divers to visit such sites. There is some evidence to suggest that growth rates of individuals at sites where they appear stunted are limited by a lack of available food (Shepherd and Hearn, 1983). By removing individuals, more food may be available to those that remain and their growth rates may, in turn, increase.

Considering the frequency of studies reporting covariation in growth and morphology of abalone, we suggest that alternative size limits appear to have the potential to improve the management of many abalone fisheries. The intense spatial variation in growth and related differences in morphology of *Haliotis rubra* in NSW, and the ease with which shell width can be measured, make a size limit based on width a potential alternative to the present length limit. The application of a width limit would allow abalone that have grown at different rates to be harvested at different lengths, essentially enforcing different length limits over very small spatial scales. As a consequence, the potentially damaging imbalance in exploitation rates among sites with different rates of growth in length would be avoided.

Acknowledgments

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An analysis of weekly fluctuations in catchability coefficients*

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Analyses of time series of commercial catch statistics are usually made with an implied assumption that catchability remains constant. Although the annual catchability from year to year may remain fairly constant, this assumption is rarely, if ever, valid for catchability within a season. Changes in catchability, abundance, and fishing all contribute to fluctuations in the catch from a fish stock (Clark and Marr, 1956; Pope and Garrod, 1975). Behavioral changes due to size or age may cause variations in catchability (Morrissy and Caputi, 1981). By examining the within-season changes in catchability, it may be possible to discern properties of a stock that are not apparent when only annual time intervals are examined.

The objective of this study was to develop a means to estimate weekly within-season catchability coefficients of a stock and to demonstrate how examination of these short-term fluctuations might be useful in a stock analysis. Atlantic menhaden, *Brevoortia tyrannus,* was selected as a model because of the availability of a time series of weekly catch-at-age data for this species.

Methods

Data

Weekly menhaden catch-at-age (in numbers) and vessel-landings data from 1968 to 1982 were made available by the Beaufort Laboratory, National Marine Fisheries Service (NMFS), Beaufort, North Carolina. Migrating menhaden stratify by age and size (Nicholson, 1971b); therefore, the stock was divided into age groups to eliminate differences in catchability due to age-specific (and size-specific) migration patterns.

Calculation of weekly abundances

Abundance estimates with constant time intervals of one week were needed to allow between-year comparisons of weekly catchability and to conform to the Beaufort Laboratory's system of reporting catches. Such short time intervals usually resulted in consecutive intervals of zero catches commonly occurring near the beginning and end of a sequence of weekly landings data for a given year and age group.

Murphy (1965) developed a method for estimating abundance and fishing mortality rates on a cohort of fish when catches are known within time intervals and when an estimate of instantaneous fishing mortality for one time interval and natural mortality for all time intervals are available. A restriction on this method is that the time intervals must be of equal duration and that each time interval must contain catches. Tomlinson (1970) presented a generalization of Murphy's method, which allowed for variable time intervals and zero catches, provided that the first and last time intervals each contain catches and that two or more consecutive zeros do not occur.

The normal method for ensuring that consecutive zero's do not occur in the catch data is to pool time intervals containing zero catches with adjacent nonzero intervals. In this study it was desirable to keep the time intervals fixed, even if it results in consecutive zeros in the catch data. A modification of Tomlinson's method was used, which allows for any number of consecutive zeros, provided that the first and last time intervals contain catches.

Extension to Tomlinson's model

A catch ratio, R_i, can be constructed between catch in the current and subsequent time interval. The ratio for interval i is given by (Eq. 4 in Tomlinson, 1970)

$$R_i = \frac{C_{i+1}}{C_i} = \frac{e^{-t_i(F_i+M_i)}E_{i+1}}{E_i}, \quad (1)$$

where C_i, C_{i+1} = number of fish caught in time intervals i, i+1;
F_i = instantaneous fishing mortality in time interval i;
M_i = instantaneous natural mortality in time interval i;
E_i, E_{i+1} = exploitation rate in time intervals i, i+1.

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If catch in time interval $i+1$ is zero, then the ratio R_i is zero and the subsequent ratio R_{i+1} is undefined. In this case, the ratio can be constructed between the current time interval and the second subsequent interval. This ratio (R_{i+1}) is given by Equation 5 in Tomlinson, 1970, as

$$R_{i+1} = \frac{C_{i+2}}{C_i} = \frac{e^{(-t_i(F_i+M_i)-t_{i+1}M_{i+1})}E_{i+2}}{E_i}. \quad (2)$$

The above equation is Tomlinson's extension to Murphy's catch equation. This can be further extended to include any number of intermediate time intervals with zero catch. A generalized form of the catch ratio between any two time intervals i and $i+k$, where the catches for all intermediate time intervals is zero, is

$$\frac{C_{i+k}}{C_i} = \frac{E_{i+k}e^{-t_i(F_i+M_i)-(t_{i+1}M_{i+1})-\cdots-(t_{i+k-1}M_{i+k-1})}}{E_i}. \quad (3)$$

Given an estimate of natural mortality rate and fishing mortality rate for the final time interval, F_i's for the previous time intervals can be solved by estimating $E_i \times \exp[t_i(F_i+M_i)]$. This can be estimated from E_{i+k} by rearranging Equation 3 as

$$E_i e^{t_i(F_i+M_i)} = \frac{C_i E_{i+k} e^{-(t_{i+1}M_{i+1})-\cdots-(t_{i+k-1}M_{i+k-1})}}{C_{i+k}}, \quad (4)$$

where C_i is nonzero, and all catches between t_i and t_{i+k} are zero. F_i may be found by iteration after inserting the result of Equation 4 in the following equation (Equation 9 in Tomlinson, 1970)

$$E_i e^{t_i(F_i+M_i)} = \frac{F_i(e^{t_i(F_i+M_i)}-1)}{F_i+M_i}. \quad (5)$$

Once the F_i's have been estimated, the E_i's can be estimated by inserting the value of the above equation into the following:

$$E_i = \frac{(\text{the value of Equation 5})}{e^{t_i(F_i+M_i)}}. \quad (6)$$

After calculating the E_i's and F_i's, the population size at the start of each time interval (N_i) can be estimated from

$$N_i = \frac{C_i}{E_i}, \text{ where } E_i <> 0. \quad (7)$$

To demonstrate the use of this extension to Tomlinson's method for solving the catch equation, the computer program MURPHY (Abramson, 1971), which implements Tomlinson's model, was modified to incorporate the extension for consecutive zeros to estimate weekly abundance and fishing mortalities for the Atlantic menhaden purse-seine fishery. The catch data were broken up into weeks and into age groups within a week.

Constant parameters used

In addition to catch-at-age data, virtual population analysis (VPA) requires estimates of instantaneous natural mortality for all time intervals and an estimate of instantaneous fishing mortality for one time interval. Natural mortality was assumed constant and a weekly value of 0.0087 (annual M=0.45) was adopted on the recommendation of the Beaufort Laboratory. Estimates of fishing mortality for the final week of landings data in each year were obtained from Table 13 of Broadhead et al.[1] for the years 1968–76 and for age groups 0–5. For age groups 6–8 the values for age 5 were used. For the years 1977–82, the average values for the years 1968–76 for each age group were used (1968–75 for age group 0). In each case, the annual value of F from the table was divided by the number of weeks in the year that had landings data to obtain a weekly F. Instantaneous fishing mortality values were probably overestimated because catch generally declined at the end of the season. However, in the backward solution to the catch equation, the value for F tends to converge toward its true value for a given M. Therefore, the error in abundance estimates due to this overestimation of F should be minor at the beginning of each year's landing data, although it may result in the underestimation of abundance toward the end.

Defining effort

An index of fishing effort was needed to calculate a catchability coefficient. The number of vessels with landings in a given week (vessel-week) is commonly used as the unit of fishing effort in studies of the menhaden purse-seine fishery and was the unit used in this study. Menhaden vessels generally operate continuously throughout all or part of the fishing season, fishing every day, as weather permits, un-

[1] Broadhead, G., C. Grimes, J. Loesch, W. Nelson, G. Sakagawa, and K. West. 1980. Report of the Atlantic menhaden population dynamics subcommittee to the Atlantic menhaden scientific and statistical committee on the status of the Atlantic menhaden stock and fishery. Unpubl. manuscr., 68 p.

less they are in port for repairs. Any time period that assumes continuous fishing and accounts for unproductive fishing days should be a satisfactory unit of fishing effort (Nicholson, 1971a). Number of landings as a unit of effort assumes continuous fishing. Although the number of days that a given vessel was fishing in a week was unknown it was assumed that variations were randomly and normally distributed.

Calculation of weekly catchability coefficients

The catchability coefficient is defined as the fraction of a fish stock that is caught by a defined unit of fishing effort (Ricker, 1975). The relation between catch, effort, abundance, and catchability is

$$\left(\frac{C}{f}\right)_t = q_t N_t, \tag{8}$$

where $(C/f)_t$ = average catch per unit of effort over period t; N_t = average abundance during period t; and q_t = catchability during period t.

The VPA estimates of abundance are for the beginning of a time period. For the short, one-week time periods used in this study, average abundance in a period is assumed to approximate $(N_t + N_{t+1})/2$. Average catch per unit of effort in a time period can be calculated as total catch divided by total effort for that period. The above equation can thus be rearranged to define the catchability coefficient as

$$q_t = \frac{\left(\frac{C_t}{f_t}\right)}{\left(\frac{N_t+N_{t+1}}{2}\right)}. \tag{9}$$

This equation was used to calculate initial weekly catchability coefficients for each age group. No catchability estimate was made for weeks in which there was no catch landed for the age group considered. Also, no catchability estimate was made if abundance estimates were not made for both the week being considered and the following week, because the average abundance during the week $(N_t+N_{t+1}/2)$ was used to estimate catchability.

Statistical analysis

Weekly abundance estimates at age were made in each year from the first week in which a catch was landed until the last. Catchability coefficients by age were estimated for each week for which there were abundance estimates for the current and subsequent weeks. Friedman's method for randomized blocks (Sokal and Rohlf, 1981) was used to test for significant differences in annual patterns of weekly catchability coefficients for each age group between years. This is the nonparametric analog to the parametric analysis of variance (ANOVA) randomized complete block design, but the rankings of the variates within each block are used rather than the actual measurements. A nonparametric test was used because the relative degree of weekly fluctuations from year to year may vary owing to biotic or abiotic factors. Thus, heterogeneity of variance between years may be expected, making a parametric model inappropriate.

Results

The Friedman's test indicated that at least one year was significantly different from the others at the 0.05 alpha level for age groups 1, 2, 3, and 4 but not significant for the remaining age groups. Subsequent multiple comparisons for these age groups with Friedman's rank sums (Hollander and Wolfe, 1973) failed to show temporal differences. These differences were therefore considered to be random variations about a mean, allowing the annual variations for each week to be averaged to determine the underlying pattern.

Plots of high, low, and mean weekly catchability were created for each age group (Fig. 1). For most age groups the range of catchability coefficients was greater at the beginning and end of the season than in the middle. The plots were examined visually for signs of fluctuation within a season. The graphs of weekly catchability showed the following pattern: the first part of the catchability curve features an initial peak followed by a rapid decline. This decline is followed by a gradual increase in catchability as the season progresses, then by a second sharp peak near the end of the season. The height of the initial peak relative to the rest of the plot is most pronounced in age-1 and age-2 fish. It becomes less pronounced and disappears altogether as the fish become older. This first peak does not occur for age-0 menhaden, which are subject to a fishery that is largely directed against catching them in the fall.

The catchability graph of age-0 menhaden differs from the other age groups. This age group is not targeted during most of the year but becomes subjected to a directed fishery off North Carolina in the fall. Catchability for this age group remains at or near zero for most of the season because no age-0 fish are being caught. Near the end of the season, it rapidly rises from zero to a peak and then quickly drops back to zero as the fishery ends.

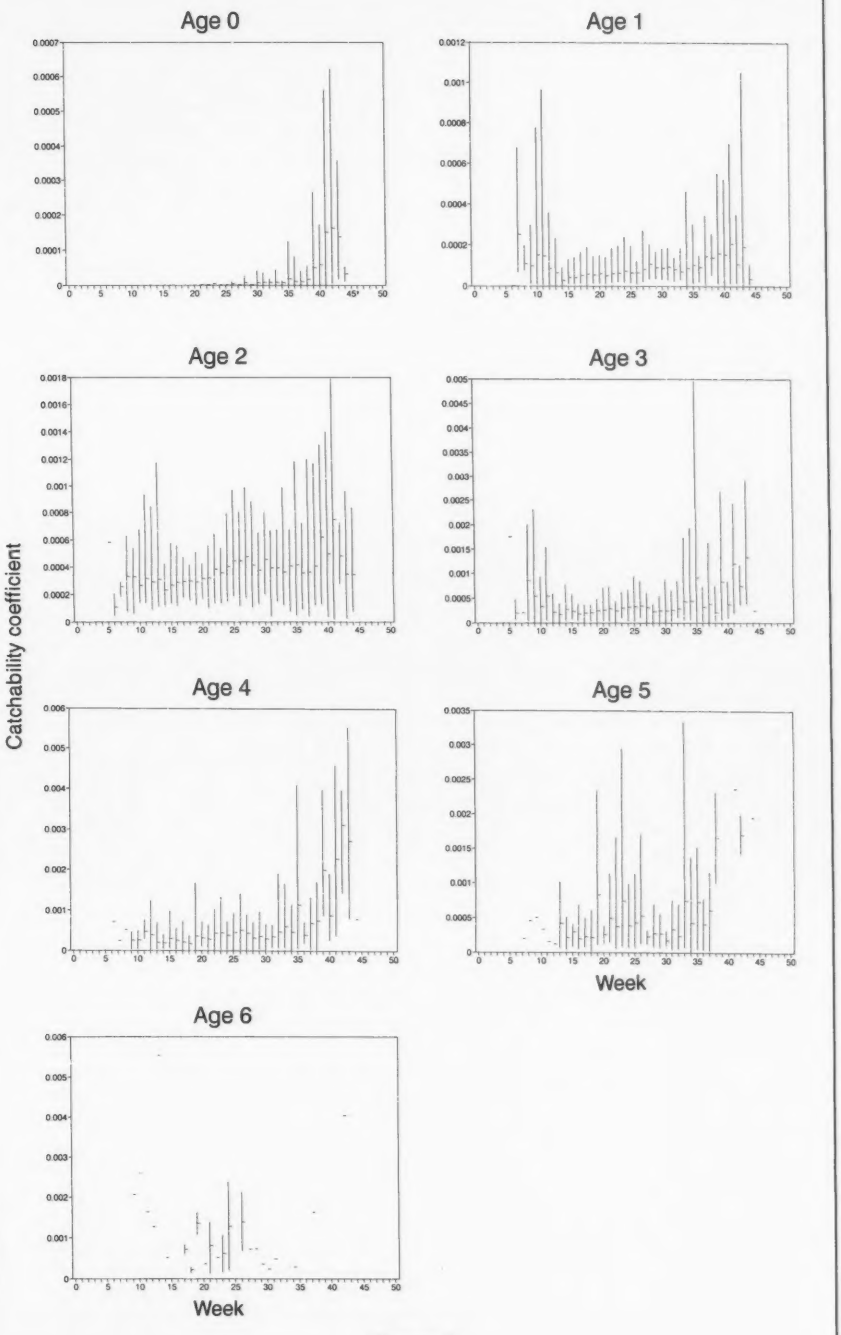

Figure 1

Mean and range of weekly catchability coefficients for Atlantic menhaden, *Brevoortia tyrannus*, from 1968 to 1982.

Discussion

Virtual population analysis assumes that there is complete recruitment for a set of age classes and that availability remains constant for all recruited age classes. The existence of sharp initial and ending seasonal catchability peaks is probably due to underestimation of abundance at the beginning and end of the season from the VPA method. This indicates that VPA can be biased when availability fluctuates. Virtual population analysis measures the "virtual" abundance, that which appears to the fishery to be there, rather than absolute abundance. Early in the season, when the menhaden are migrating into the fishing area from their wintering grounds, only part of the stock is available for exploitation. Changes in availability, or accessibility, can affect the catchability coefficient (Cushing, 1968). Marr (1951) showed that catchability is directly related to availability. However, because VPA assumes that there is full availability, abundance is underestimated. If the abundance is underestimated, then the catchability coefficient will be overestimated (Shardlow and Hilborn, 1985).

Theoretically, this first peak should extend to infinity prior to the start of the season when VPA is used to estimate abundance, because availability at this point in time is zero. If abundance had been measured with a method independent of the fishery catch statistics, such as mark-recapture, catchability estimates would have been based on absolute rather than on virtual abundance and there would not have been an early season peak. The rise from zero or near-zero catchability which occurs in many of the plots, particularly with older age groups, may be due to an earlier or faster migration of these age groups into the fishing area or to more complete recruitment of the age group at the start of the season. Younger age groups are not completely recruited into the fishery, but by age 2, the menhaden are fully recruited into the Atlantic coast purse-seine fishery (Atlantic Menhaden Management Board, 1981). If availability is at or near maximum by the time of the first catch, VPA will not underestimate abundance, and consequently catchability will not be overestimated. One advantage of examining within-season fluctuations of catchability, therefore, may be to assess when the stock becomes available to the fishery.

After the initial peak, a gradual rise in catchability can be seen as the season progresses, most likely due to a decrease in abundance during a period of full availability. This observation is consistent with Schaaf (1975), who reported a logarithmic inverse relation between annual values of catchability and abundance of menhaden. An increase in this rate might result if stock abundance during the season were decreasing faster than normal, and it would then be an indicator of overfishing.

The pattern of catchability for age-0 menhaden differs from that of the other age groups in that there is no initial peak and landings begin much later in the season (Fig. 1). Age-0 menhaden are fished extensively in the North Carolina fall fishery which is largely directed toward these fish. Paloheimo and Dickie (1964) stated that when fishermen selectively apply their effort toward some schools, the result is variance in the catchability coefficient depending on age, species, and relative abundance. This effect is apparent in the plot of average weekly catchability coefficient for age-0 menhaden. When the age-0 menhaden, commonly referred to as "peanuts," migrate out of Virginia and North Carolina estuaries, they become readily available close to shore where they dominate the landings, usually in December and January.

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Temperature influence on postovulatory follicle degeneration in Atlantic menhaden, *Brevoortia tyrannus*

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The occurrence of postovulatory follicles within the ovaries of fish is a positive indication of spawning, because they are the evacuated follicles following ovulation. Therefore, their frequency of occurrence may be used to test factors influencing reproduction. For example, postovulatory follicles can be used to estimate spawning frequency, which in turn is used to estimate spawning biomass (Hunter and Macewicz, 1985). Their state of degeneration can be assessed from histological sections of the ovary to estimate the time elapsed since spawning for females sampled in the wild. In addition, the occurrence of postovulatory follicles might be useful to test hypotheses about events that may trigger spawning and benefit larval transport (see Taylor, 1984; Checkley et al., 1988).

A requisite for applying this histological method of determining spawning frequency is validation of the duration that postovulatory follicles can be detected in field samples. This has been done through closely timed observations of spawning in the field and by laboratory-induced spawning and subsequent sampling of female gonads (Hunter and Macewicz, 1985). Laboratory spawning offers more certainty in determining the time of spawning and facilitates more precise measurement of the degeneration time of postovulatory follicles. Uncertainty regarding the duration of postovulatory follicles has led to questions about estimates of spawning frequency (Brown-Peterson et al., 1988; Fitzhugh et al., 1993; and Goldberg et al., 1984). Variation in the duration of postovulatory follicles may be largely due to the particular species involved and its preferred spawning temperature (Hunter and Macewicz, 1985).

Atlantic menhaden spawn across a wide geographic range of U.S. coastal Atlantic waters (Cape Canaveral, Florida, to Martha's Vineyard, Massachusetts) and probably over a wide range of temperature as well (Judy and Lewis, 1983). Eggs have been collected between the 15° and 20°C surface isotherms in the mid-Atlantic Bight (Kendall and Reintjes, 1974). We wished to examine differences in postovulatory follicle duration and age at stage due to temperature in Atlantic menhaden. As a preliminary step to future estimation of spawning frequencies, our objective was to characterize postovulatory follicle degeneration and validate postovulatory follicle duration for Atlantic menhaden induced to spawn at different temperatures in the laboratory.

Materials and methods

Adult menhaden were collected near Harker's Island, North Carolina, between mid-August and mid-September 1988, 1990, 1991, and 1992. During each period, menhaden were maintained in outside tanks under ambient flow-through conditions until mid-October to mid-November when they were moved to inside tanks to begin conditioning for spawning. We induced spawning in either December (1990) or March (1988, 1991, 1992) with methods reported by Hettler (1981). Menhaden of both sexes were conditioned to spawn by means of intraperitoneal injections of human chorionic gonadotropin (HCG) and carp pituitary extract (CP). We gave injections between 0800 and 1000 hours on successive days, and spawning usually occurred the night following the second (CP) injection.

Spawning was induced under three temperature regimes; 14.8–15.7°C for one group in December 1990; 17.9–18.2°C for one group in March 1992; and 19–20°C for groups in March 1988, December 1990, and March 1991. Groups of menhaden ranged from 22 to 31

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individuals and the male to female ratio was about equal. In December 1990, only 12 individuals were induced to spawn at the coldest temperature regime (7 were subsequently identified as females). For each group, acclimation and holding temperatures were held constant prior to spawning and for the week following spawning.

The time of spawning was estimated the following morning when eggs were collected and identified to stage (Ferraro, 1980). Males were identified by the presence of free-flowing milt just prior to the CP injection and were marked by clipping the left pectoral fin. Females (identified as not having a fin clip) were sampled up to 4 days following spawning and killed in a solution of MS-222. We excised a tissue section from the middle right ovarian lobe from each female and fixed it in 10% neutral buffered formalin. Tissue samples were dehydrated, embedded in paraffin, sectioned, stained with Gill's hematoxylin and eosin for histological observation. Our interpretation of the histological states of the postovulatory follicles follows Hunter and Macewicz (1985), and the prominent features we observed are summarized in Table 1.

Results and discussion

The postovulatory follicle, which is the evacuated follicle remaining in the ovary following ovulation of the hydrated oocyte, is characterized by an outer thecal layer and an inner epithelial granulosa layer (Fig. 1). Many species show similar features in postovulatory follicle degeneration (Hunter and Macewicz, 1985) to those that we noted for Atlantic menhaden. Onset of degeneration was evident when vacuoles and eosinophils were detected within the postovulatory follicle (Fig. 1A). The granulosa layer appeared contorted or folded but the granulosa cells and their nuclei imparted a linear or cordlike appearance (Fig. 1A). Initially, the lumen was apparent but narrowed and became less distinct with time (Fig. 1, B and C). We also noted that the linear arrangement of the granulosa cell nuclei became less distinct with time (Fig. 1B). Vacuolization of the follicle increased (Fig. 1C), and a point was reached when the lumen was no longer evident. The postovulatory follicle became reduced in size but the folded appearance of the granulosa layer remained evident and aided in identifying the postovulatory follicle (Fig. 1C). We used this point in degeneration to define the postovulatory follicle duration because as the postovulatory follicle aged further (e.g. Fig. 1D), there were no exact features that could distinguish it from old atretic follicles (preovulatory follicles) that remain after an intact oocyte undergoes atresia (Goldberg et al., 1984; Hunter and Macewicz, 1985). While atresia of oocytes occurs predominately at the end of a spawning season, it is common to observe some oocytes undergoing atresia throughout the spawning season (Hunter and Macewicz, 1985). We also observed some atresia of vitellogenic oocytes in our samples. Since preovulatory follicles can be present and at some point are not distinguishable from postovulatory follicles, we can only estimate the duration that the postovulatory follicles may be identified.

The 54 females sampled after spawning from the three temperature regimes ranged in size from 200 to 250 mm fork length which is typical of 2 to 3 yearolds (Nicholson and Higham, 1964). All females (n=35) from the warm regime (19–20°C) that were sampled within about 40 hours of spawning (determined from the collection and identification of stages of fertilized eggs) displayed detectable postovulatory follicles (100% spawned). Eleven of the twelve females sampled from the 17.9–18.2°C series displayed postovulatory follicles (92% spawned). Six females from the cold series (14.8–17.7°C) contained vitellogenic oocytes, indicating an advanced reproductive state; one female possessed cortical alveolar stage oocytes—an immediate precursor to the vitellogenic stage (deVlamming, 1983). However, only 4 of 7 females from the cold series possessed detectable postovulatory follicles (57% spawned). The reduced temperatures appeared to diminish our ability to induce spawning.

Table 1

Distinguishing features for the stages of postovulatory follicle degeneration[1] in Atlantic menhaden, *Brevoortia tyrannus*.

Stage	Characteristics of postovulatory follicles
1	Granulosa cells are aligned and granulosa-layer nuclei appear linear in orientation. Some lymphocytes and vacuoles may appear in the postovulatory follicle, signaling initial degeneration.
2	Loss of linear arrangement of granulosa layer nuclei; cell membranes and columnar/cuboidal shape of granulosa layer is no longer distinct. Lumen is still clearly visible.
3	Although irregular postovulatory follicle shape is still detectable, fewer folds are apparent as the lumen becomes reduced and is no longer distinct.
4	Linear appearance of the granulosa layer is no longer distinct; postovulatory follicle not readily distinguished from atretic oocytes.

[1] Adapted from Hunter and Macewicz, 1985.

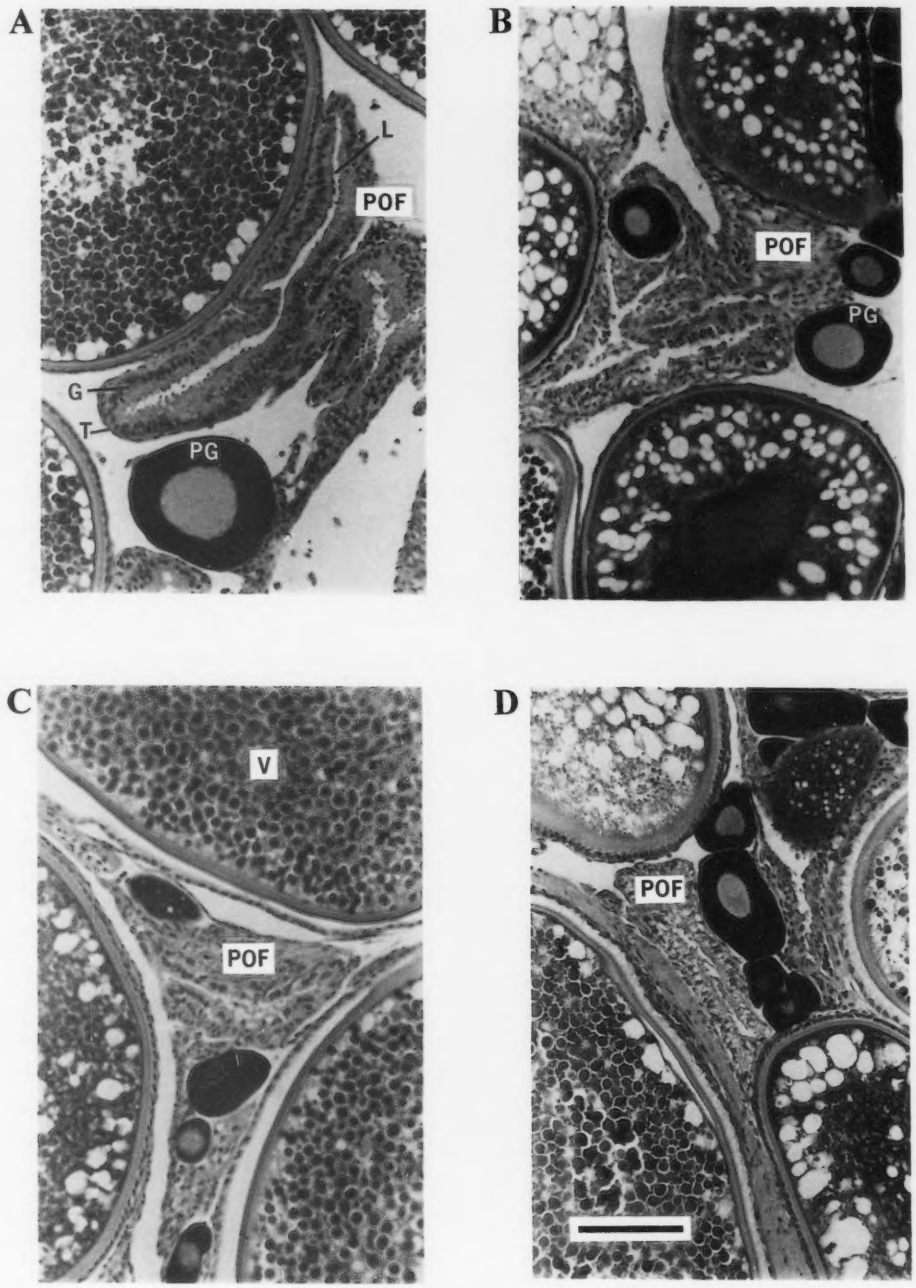

Figure 1

Postovulatory follicles (POF's) from female Atlantic menhaden held at 20°C. Elapsed time from estimated spawning is (**A**) 11 hours, (**B**) 21 hours, (**C**) 38 hours, and (**D**) 45 hours. Features characterizing postovulatory follicles are as follows: L = the lumen; G = the granulosa layer; and T = the outer thecal layer. Vitellogenic oocytes are denoted by (V) and primary growth oocytes are denoted as (PG). The scale bar represents 0.1 mm.

All spawning was estimated to have occurred between 2100 and 0200 hours and time from spawning was recorded at each sampling period. We compared histological states associated with these sampling periods by standardizing the time of spawning (midnight, hour-0; Fig. 2). In general, events associated with induction of spawning slowed down in the cold temperature regime. Spawning at 14.8–15.7°C occurred about 63 hours after HCG injection and about 39 hours after CP injection. However, within the warmest series, spawning occurred about 34 and 11 hours, respectively, after HCG and CP injections.

We saw characteristics of initial follicle degeneration about 6 to 12 hours after spawning for all three temperature regimes (Fig. 2, Table 1). There was an apparent difference in overall duration of postovulatory follicles between the high and low temperature regimes. Filling of the lumen (stage 3) was evident at the warm regime by about 21 to 46 hours (Fig. 2). At 19–20°C, postovulatory follicles were difficult to distinguish (stage 4) as early as 36 hours, but at the two colder regimes, postovulatory follicle degeneration was not as advanced even at 58 hours (e.g. stage 3, Fig. 2). Postovulatory follicle duration at 15°C is probably longer than 60 hours after spawning.

Transition to successive atretic stages was apparently faster at the warmest temperature and there was some overlap of atretic stages at a given time following spawning. For example, stages 1, 2, and 3 were observed at 20 hours from females held at 19–20°C (Fig. 2). This overlap may be due to variation in degeneration rates among females, the subjectivity of stage classification across a continuum of follicle degeneration, or to variation in the exact time of ovulation among females (because time from spawning was estimated for all the females in a group from a sample of fertilized eggs). A more precise analysis of the durations for the various stages of atresia would have been facilitated by sampling each group at constant intervals after the spawning of eggs and by using a larger sample size—particularly for the coldest treatment.

Observations of postovulatory follicle duration vary for species that spawn at different temperatures. We observed durations ranging from about 36 to over 60 hours for Atlantic menhaden spawning from 15 to 20°C. At similar temperatures (13 to 19°C), northern anchovy, *Engraulis mordax*, Peruvian anchovy, *Engraulis ringens*, and Pacific sardine, *Sardinops sagax*, have postovulatory follicles that last about 48 hours (Hunter and Macewicz, 1985). Skipjack tuna, *Katsuwonus pelamis*, and Hawaiian anchovy, *Encrasicholina purpurea*, spawn at approximately 25°C and have postovulatory follicles that last about 24 hours (Hunter et al., 1986; Clarke, 1987). The

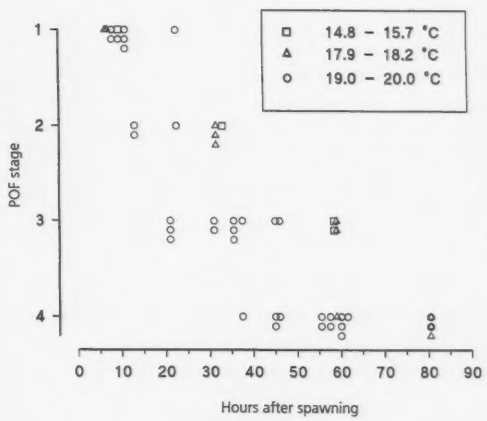

Figure 2

Chronology of spawning and postovulatory follicle (POF) degeneration for three temperature series (14.8–15.7°C, 17.9–18.2°C, and 19.0–20.0°C). Postovulatory follicle stages (1–4) are described in Table 1. All spawning times are set to midnight (hour-0) in order to make contrasts across temperature series (see text). Symbols slightly offset along the y-axis at each stage of degeneration correspond to multiple fish sampled at the same time.

dragonet *Callionymus enneactis* spawns at 28–30°C and has a postovulatory follicle duration less than 15 hours (Takita et al., 1983). Collectively, these observations confirm that increasing temperatures decrease the time that postovulatory follicles can be detected in fishes.

The ability to identify the stage of postovulatory follicles in order to determine spawning frequencies becomes more important as their duration increases. If postovulatory follicles are known to last less than 24 hours, females possessing them can be defined with certainty as having day-0 postspawning ovaries for purposes of estimating spawning frequency. Hunter and Goldberg (1980) and Hunter and Macewicz (1985) developed this approach on the basis of the appearance of various features and assigned day-0 and day-1 classifications to fish known to have postovulatory follicle durations of about 48 hours. However, if durations are known to be longer, knowledge of the age of particular features of postovulatory follicles becomes more critical in classifying postspawning ovaries. We focused on the alignment of the granulosa layer (and nuclei), on the presence of vacuoles, and the appearance of the lumen for identifying stages because these features were easily recognizable in Atlantic menhaden postovulatory follicles and could be used to classify fairly discrete

stages (Table 1). In Atlantic menhaden spawning at about 20°C, disappearance of the lumen of the postovulatory follicle after loss of alignment of the granulosa layer (transition from stage 2 to 3) distinguished day-0 from day-1 postspawning ovaries. However, in several other species, features such as pycnotic nuclei, thickness of the thecal layer, and separation of the thecal and granulosa layers are diagnostic for classification of postspawning ovaries (Goldberg et al., 1984; Hunter and Macewicz, 1985; Agarwal et al., 1992).

Postovulatory follicle durations in *Engraulis* species spawning naturally or in those induced pharmacologically to spawn at similar temperatures are equivalent (Hunter and Goldberg, 1980; Goldberg et al., 1984) suggesting that laboratory observations can be used to access spawning frequencies of fish in the wild. Our estimates of the durations of particular features of postovulatory follicles must be considered preliminary on the basis of our small sample size, particularly for the 14.8–15.7°C treatment fish. However, our general finding that postovulatory follicle duration within Atlantic menhaden can vary from 36 to probably more than 60 hours corresponding to a 5°C range in temperature, supports the view that temperature should be an important consideration affecting spawning-frequency estimation in field surveys.

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Size structure of mutton snapper, *Lutjanus analis*, associated with unexploited artificial patch reefs in the central Bahamas

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The mutton snapper, *Lutjanus analis* (Cuvier, 1828) (Pisces: Lutjanidae), is an important component of shallow water reef fisheries in the tropical western Atlantic (Bortone and Williams, 1986). However, overfishing of shelf-edge spawning aggregations has contributed to a major decline in landings and, in some locations off Florida and Cuba, to a total collapse of the fishery (Brownell and Rainey, 1971; Gulf of Mexico Fishery Management Council, 1992). Much of what we know about *L. analis* (i.e. age and growth, reproductive, and trophic biology) is based on samples from commercial and recreational catches (Rojas, 1960; Erhardt and Meinel, 1977; Erhardt, 1978; Pozo, 1979; Claro, 1981, 1983; Mason and Manooch, 1985; Palazón and González, 1986). Quantitative behavioral studies are few (Mueller, 1994; Mueller et al., 1994), and field investigations concerning the population structure of *L. analis* under natural conditions are lacking.

Visual censuses are useful for comparison of temporal changes in the size structure of fish populations on exploited reefs with those of fish populations on unexploited reefs (Craik, 1981; Russ, 1985). However, such methods have several inherent biases. At best, visual censuses provide reasonably precise records of the fish fauna that are not greatly influenced by conditions of water clarity (Sale and Douglas, 1981). Because counting all the fish in a given area is nearly impossible, size frequencies derived from visual censuses should be used for relative comparisons between populations (Craik, 1981). Using visual census techniques, I describe a preliminary study of seasonal variation in the size structure of *L. analis* on unfished reefs for the purpose of making comparisons with fish of this species that are subjected to fishing pressure.

Materials and methods

Size frequencies of *L. analis* associated with two artificial patch reefs off Lee Stocking Island, Exuma Cays, Bahamas (23°46.21'N, 76°06.59'W), were monitored during snorkeling excursions between 22 May 1991 to 14 December 1992. The primary reef (reef 1, area=491 m^2) was located in a shallow (2.7 m), moderately dense *Thalassia testudinum* Koenig meadow (biomass=40–80 g dry wt·m^{-2}, Stoner and Sandt, 1991), whereas a smaller reef (reef 2, area=78 m^2) was located in deeper water (4 m), 107 m west of reef 1. A distinct, gently sloping contour in the seagrass bed was evident between the two reefs. Both reefs were composed of man-made materials and had a sparse cover of the living corals *Millepora alcicornis* Linnaeus and *Porites porites* (Pallas). The position of and distance between the reefs were determined by using a Magellan™ global positioning system unit. Reef areas were determined by using a waterproof measuring tape during SCUBA dives. Although natural patch reefs occurred in the area, this site was selected because it was unexploited and had a large number of *L. analis* associated with the reefs.

Data were collected every 4–11 weeks, only during the flood tide (greatest water clarity) between 0600–1900 h (daylight hours) to maximize visibility. By comparing my position with the known distance between reef structures at reef 1, I inferred that the maximum limit of my visibility during flood tide was approximately 20 m. Current directions of the flood and ebb tides at the study site were west (180°) and east (0°), respectively. During flood tide, I was able to drift (>30 cm per second) from reef 2 to reef 1 in five minutes or less. Using the natural water flow and bottom topography as references, I followed the same path between the two reefs during each census. All fish observed within 20 m (the approximate limit of my visibility) to either side or end of this quasi-transect (total search area including reefs ≈5,600 m^2) were counted and measured. Fork lengths (FL) were estimated visually within 5 m of fish by comparing subjects to a known scale, the 30-cm length of a hand-held underwater slate. Fish were placed into one of three size classes relative to my slate: 20, 30, and ≥40 cm FL (shorter than, equal to, and longer than the slate, respectively). *Lutjanus analis* swam into the current (positive rheotaxis); therefore once I had passed

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a fish, I did not encounter that fish again during the drift. To confirm the accuracy of my underwater FL estimates, I compared markings on my slate (1-cm increments) with structural relief that *L. analis* rested on or passed by at reef 1. I repeated this practice until I could discern between the three size classes ±5 cm from distances up to 5 m away.

On each sampling date, I performed three replicate drifts from reef 2 to reef 1. Size frequencies were derived from the largest number of fish counted in each of three size classes, irrespective of replicate, because the number of fish in each size class was at least equal to the greatest number of that size class seen during a single drift (Sale and Douglas, 1981).

Results and discussion

Four individual *L. analis* were recognized from census to census for periods up to one year. Fish were identified by body size, scars, fin anomalies, or shape of the black upper-body spot. However, owing to the wary nature of *L. analis*, it was difficult to remain within close proximity of subjects to identify adequately all fish by this method. Although individuals were considered resident, it is possible that others were transient or wandering fish. Still, my observations are consistent with a previous study (Beaumariage, 1969) that indicated little movement in adult *L. analis*.

On each sampling date, up to 56 *L. analis* were counted and measured at the study site. Fish ranged in size from 15 cm FL (half the length of my underwater slate) to 65 cm FL (>twice the length of my slate). Small (20-cm-FL), medium (30-cm-FL), and large (≥40-cm-FL) *L. analis* were aged 1+ yr, 2+ yr, and 3+ yr, respectively (sensu Claro, 1981; Mason and Manooch, 1985). The number of small and medium-size fish observed varied from 6 to 24 and 12 to 25, respectively. The number of large fish never exceeded 13 (Table 1). From April to July, fish sizes were normally distributed; however, during August, fish sizes became negatively skewed. On 23 February 1992, water clarity was extremely poor (<5 m), which may account for the low number of small fish recorded on this date (Table 1).

The causes for seasonal variation in the size structure of *L. analis* are difficult to isolate from my observations; however, some inferences can be drawn from previous studies. For example, the increase of small fish in late August (Table 1) corresponds well with the peak recruitment to seagrass beds reported for juvenile *L. analis* (<7 cm FL) during August (Springer and McErlean, 1962) and September (García-Arteaga et al., 1990). Jones (1990) described a similar pattern in ambon damselfish, *Pomacentrus amboinensis*, Bleeker, 1868, and showed that adult densities increased in proportion to juvenile recruitment success after a two-year period (=maturation time).

The simultaneous decrease in medium-size fish during August (Table 1) is not easily explained. The population structure of unexploited reef fish is determined by a complex sequence of events that includes recruitment, demographic changes (i.e. mortality, migration, and growth), and ecological processes such as habitat structure, resource availability, and intraspecific competition (Jones, 1991). For instance, variable patterns in growth can have a major and direct influence on the size structure of a population (Jones, 1991). Individuals that grow faster may subordinate conspecifics and establish a dominance hierarchy (Forrester, 1990). Once established, hierarchies are often extremely stable (Morse, 1980). For example, where individually recognized recruits were followed over time, juvenile humbug, *Dascyllus aruanus* (Linnaeus, 1758), never outgrew other group members in size during an eight-month period (Forrester, 1990).

Lutjanus analis exhibits much variation in length for a specific age (Mason and Manooch, 1985) but matures sexually at fork lengths above 38 cm (Claro, 1981). In the central Bahamas, *L. analis* form groups of variable-size fish that occupy seagrass meadows

Table 1

Size frequencies of mutton snapper, *Lutjanus analis*, sampled from a population associated with two artificial patch reefs located off Lee Stocking Island, Exuma Cays, Bahamas. Fork lengths were estimated visually by comparing fish to a known scale (30-cm length of a hand-held underwater slate) and are ±5 cm.

	Fork length (cm)			
Sample date	20	30	≥40	Total no. sampled
22 May 91	6	21	8	35
1 July 91	16	25	5	46
29 July 91	11	24	11	46
24 August 91	23	12	6	41
5 October 91	16	12	10	38
7 December 91	22	13	6	41
23 February 92	6	20	10	36
20 March 92	23	18	7	48
19 April 92	8	23	13	44
18 May 92	10	22	6	38
17 June 92	12	22	5	39
16 August 92	24	18	9	51
26 October 92	19	17	9	45
14 December 92	18	25	13	56

near inlets and patch reefs (Dennis[1]). Size-specific asymmetries in both social and foraging behaviors suggest that these groups form dominance hierarchies (Mueller, 1994; Mueller et al., 1994). Assuming that large *L. analis* did not migrate from the study site (Beaumariage, 1969; author's personal observ.) and given that higher proportions of aggressive encounters occur among medium-size and large fish compared with small fish (Mueller et al., 1994), it is possible that the few large, dominant *L. analis* limited the number of medium-size fish on site through social interactions (sensu Doherty, 1983; Jones, 1987; Forrester, 1990). However, because empirical evidence is not available to support this conclusion, experiments should be designed to test whether large *L. analis* are a limiting factor.

Changes in the size structure of *L. analis* between 1991 and 1992 (i.e. the shift from small towards medium-size fish; Table 1) may also be related to growth. For example, small *L. analis* (1+ yr) feed proportionally more often than medium-size or large fish during daylight hours (0600–1730) and are involved in very few intraspecific encounters (Mueller et al., 1994). By limiting their interactions with conspecifics, small fish ostensibly have more time and energy available for growth (≥0.8 cm/mo during years 1 and 2; Claro, 1981; Mason and Manooch, 1985). Further studies may be designed to test this hypothesis.

In conclusion, managers of reef fisheries are challenged with determining whether shifts in the size structure of populations are due to normal recruitment and postrecruitment events or to fishing pressure. For example, low abundance of a certain size class may be due to intraspecific competition (Doherty, 1983; Jones, 1987; Forrester, 1990) or growth rather than to the effects of fishing. However, previous studies also indicate lower average size and abundance of fish captured on exploited reefs as opposed to unexploited reefs (see review by Russ, 1991). I have provided evidence of seasonal variation in the size structure of *L. analis* associated with unfished reefs. Although potential biases exist, this information should be useful for making relative comparisons with analogous populations subjected to fishing pressure.

Acknowledgments

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Occurrence and group characteristics of minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay

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The minke whale, *Balaenoptera acutorostrata*, is one of the smallest of the baleen whales. Despite exploitation by the whaling industry in recent years, comparatively little is known about the biology and behavior of this species. The minke has a cosmopolitan distribution, although recent biochemical studies suggesting large genetic differences between oceanic populations (Amos and Dover, 1991; Hoelzel and Dover, 1991; van Pijlen et al., 1991; Wada and Numachi, 1991; Wada et al., 1991) have cast some doubt on the long-held belief that all populations constitute a single species. As is the case for most baleen whales, minke whales appear to migrate to high latitudes in the summer for feeding and to travel to tropical waters in the winter for birthing (Horwood, 1989; Mitchell, 1991). However, specific breeding grounds have yet to be unequivocally identified, and it is unknown whether both sexes and all age classes in a population undertake the migration to low latitudes. In some temperate, subtropical, and tropical areas, minke whales are observed throughout the year (Ivashin and Votrogov, 1981; Best, 1982; Gong, 1987; Stern, 1990), although it is unclear whether these sightings represent year-round residency on the part of particular individuals or a more general movement through the area by members of one or more populations.

In recent years, much has been learned about other mysticetes through long-term studies based on the identification of individual whales (see Hammond et al., 1990). Unfortunately, minke whales lack the great variability in natural markings that have facilitated detailed investigations of larger confamilials (such as humpback whales, *Megaptera novaeangliae*). This, together with the difficulty of photographing them owing to their small size and great speed, has hindered studies based on photographic identification, although studies of small localized populations have been possible (Dorsey, 1983; Dorsey et al., 1990; Stern et al., 1990). In general, however, studies of free-ranging minke whales have been few, and their population structure, social organization, and migratory movements remain poorly understood.

Minke whales are commonly observed in the waters of Massachusetts Bay and Cape Cod Bay in New England, and since 1979, sightings of this species have been routinely recorded from both commercial whalewatching vessels and dedicated surveys. In this paper, sighting records are examined in an effort to describe the temporal distribution, seasonal abundance, and feeding behavior of minke whales in this region. These data are then compared with information reported for this species from other areas, notably within the North Atlantic.

Methods

Study area

The study area includes the coastal region dominated by Cape Cod Bay and Massachusetts Bay along the northeastern coast of the United States (Fig. 1). Cape Cod Bay is a semi-enclosed sandy basin with a maximum depth of 60 m. Massachusetts Bay lies north of Cape Cod; depths range from 40 m to 100 m except on Stellwagen Bank, an elongated glacial feature of sand and gravel approximately 25 km in length, which has a minimum depth of 18 m.

Effort

Data were collected between 1979 and 1992. The total number of cruises conducted during this period was 10,249 (this figure excludes those made in certain weather conditions, as noted below); of these, 9,728 (94.9%) were made from 30-m commercial whalewatching vessels operating between April and October of each year from Provincetown, Massachusetts. Additional cruises (n=374) were made from a 12-m diesel-powered research vessel beginning in the autumn of 1983, and 77 cruises were made from a 14-m auxiliary ketch beginning in the autumn of 1985. The remaining non-whalewatch cruises were made primarily from a 5-m inflatable boat. Because virtually all of the whalewatching trips were approximately four hours in length,

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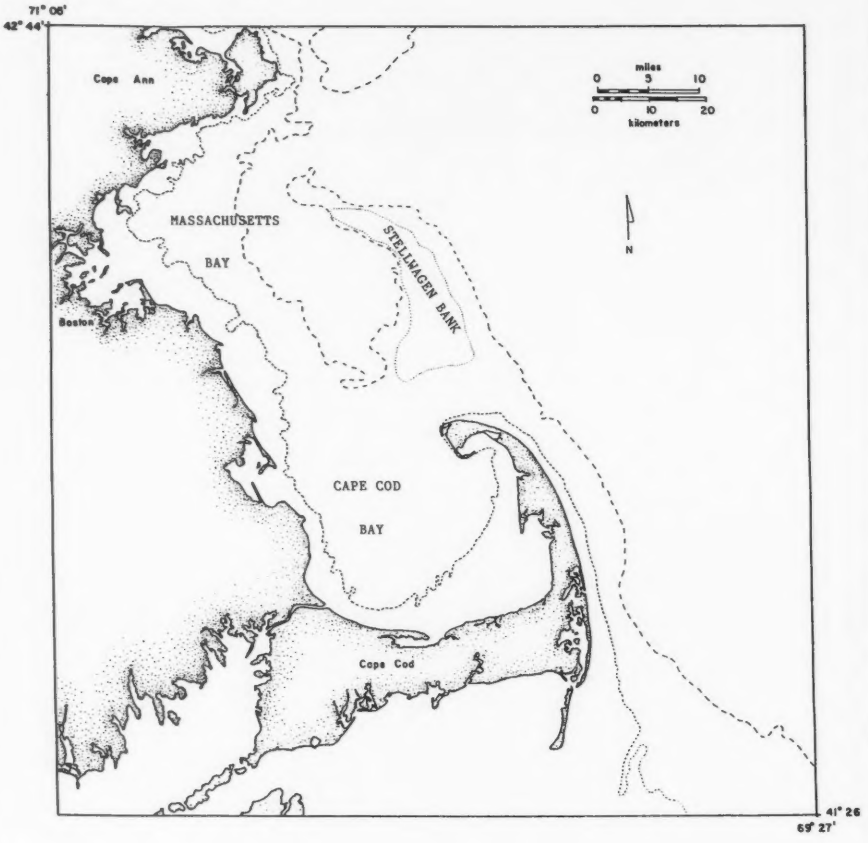

Figure 1

Map of minke whale, *Balaenoptera acutorostrata*, study area: Massachusetts Bay and Cape Cod Bay are located off the northeastern coast of the United States.

all cruises of eight hours or more were broken into separate four-hour blocks in an attempt to standardize temporal effort.

Cruises aboard the 12-m research vessel ran four fixed tracks in Cape Cod Bay between January and May each year. The tracks ranged from six to nine nautical miles in length and were approximately four nautical miles apart. These cruises searched specifically for North Atlantic right whales, *Eubalaena glacialis*; however, all marine mammal sightings were recorded. Owing to frequent unfavorable weather, the tracks were not surveyed equally; effort was concentrated mainly in the more sheltered eastern portion of the Bay. Cruises aboard the 14-m ketch occurred throughout the year and ran either four fixed tracks on Stellwagen Bank or directed searches in areas where large concentrations of whales had been recently reported or were known to have occurred in the past. The fixed tracks covered the southern portion of Stellwagen Bank, although two of the tracks extended northward to include the northwest corner of the Bank. The tracks on the southern portion of the Bank ranged from six to nine nautical miles in length, all tracks being approximately three nautical miles apart from one another. Again, all cetacean sightings were noted, although the majority of these cruises were directed primarily toward humpback whales. The remaining nonwhalewatch cruises were nonrandom, searching areas where large numbers of whales had been recently

reported. All whalewatching cruises were nonrandom and search tracks for these cruises were generally decided by the captain of the vessel.

Search effort was based on four-hour trips. It was not possible to quantify precisely observer effort; time spent searching inevitably varied somewhat between trips. However, because at least one observer was searching for whales constantly for the duration of each cruise (both on the whalewatching cruises and dedicated surveys), it is unlikely that significant differences existed in effort between months or years. Furthermore, because all trips were primarily focused on larger mysticetes, virtually all sightings of minke whales were opportunistic; consequently, search effort towards this species was effectively even throughout the study period. To minimize the possibility that minke whales were present but not sighted owing to bad weather conditions, all cruises conducted in fog or in sea states above Beaufort 4 were excluded from analysis. The total number of cruises for each month of all years is summarized in Table 1.

The following information was routinely collected: date, time, location (by using LORAN-C) and, where determinable, group size and behavior. Although photographs were occasionally taken during this study, the resulting data are not discussed here.

The following terms are used in this paper: **singleton** refers to a lone animal, **group** refers to two or more animals that were considered associated if they were swimming side by side and were generally coordinating their speed and direction of movement during their surfacing and diving behavior. Animals that were farther apart and did not show such coordination of movement were not considered associated. It is possible that two or more minke whales that were not side by side were in acoustic contact and therefore associating; however, such associations are impossible to identify in the field and were not considered in this study. **Feeding** refers to a whale observed with its mouth open or lunging at the surface where prey was visible in the water. It is highly likely that there were other instances in this study when feeding occurred below the surface but could not be observed; consequently, the feeding rates reported here should be considered minimum values. **Calf** refers to an animal considered to be a first-year calf if it was observed in close association with a large whale and was not more than half the apparent length of the latter (presumed to be the mother).

Results

Temporal distribution

There was a significant difference in the sighting rate of minke whales (number of whales observed per trip) from year to year ($\chi^2_{13} = 2188.7$, $P<0.001$); the maximum sighting rate was recorded in 1989 and the minimum in 1982 and 1986 (Fig. 2). Minke whales were observed in all months except January and February and showed significant differences in abundance by month (pooled over years) (Fig. 3). Pairwise comparisons of mean monthly values for the period of greatest effort (March through October) were conducted by using a one-way analysis of variance and are revealed in Table 2. There were no significant differences in the number of sightings between the months of March, April, May, and June (hereafter collectively termed "spring"), nor between July, August, September, and October (hereafter referred to as "summer-autumn") (Table 2). However, three of the four months of spring differed significantly from those of summer-autumn in all pairwise comparisons. The exception was March, for which sighting rates were not significantly different from those of any other month.

Calves

Only three calves were observed during the entire study period. Each sighting occurred at a different time of year: 8 May 1981, 3 October 1989, and 28 August 1991. Two of the calves were part of a pair, and the third was part of a group of three.

Table 1

The number of cruises conducted each year and each month for all years combined (1979-92) for minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay. Cruises in fog or where the sea state exceeded Beaufort 4 were excluded.

	Year													
	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
No. of cruises	127	207	414	517	630	723	789	878	875	972	989	979	1110	1039

	Month (all years combined)											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
No. of cruises	26	57	114	532	1409	1625	2091	2118	1415	793	44	25

Group-size frequency

A total of 5,806 minke whale sightings were recorded for which the group size could be reliably determined. Observed group-size frequency ($\bar{x}$=1.06, SD=0.315) for singletons (n=5,536) was 95.3%, for pairs (n=223) 3.8%, and for trios (n=46) 0.8%. With the exception of a single group of five whales, no groups larger than three were observed during this study.

Feeding behavior

A total of only 27 (0.4%) of 6,266 sightings involved confirmed feeding at the surface. These sightings occurred in all months between May and October inclusively. In 24 of the 27 sightings of feeding, group size was recorded: single animals accounted for 21 (87.5%) of these, two sightings involved pairs, and one sighting a group of three whales.

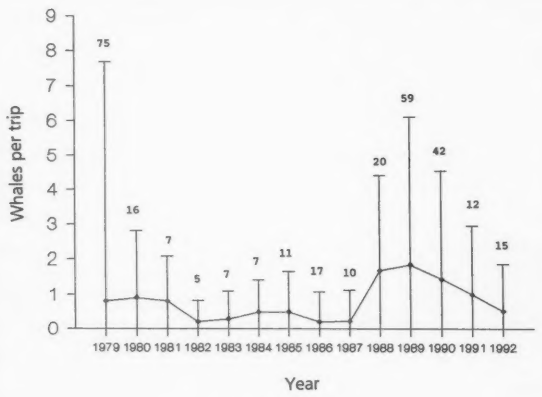

Figure 2

Observed variations in occurrence (mean and standard deviation) of minke whales, *Balaenoptera acutorostrata*, by year (1979–92) in Massachusetts Bay and Cape Cod Bay. Numbers above the bars represent maximum value for any one trip in that year.

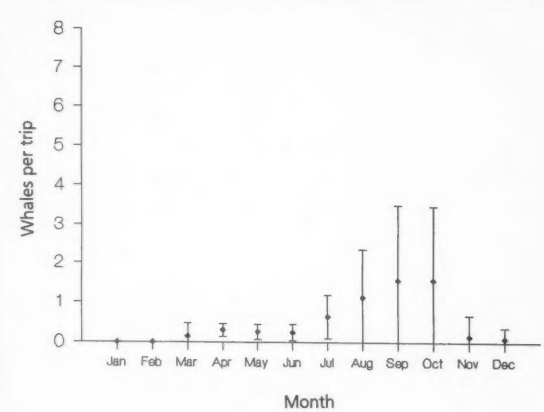

Figure 3

Observed variations in occurrence (mean and standard error) of minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay by month for all years (1979–92) of the study.

Discussion

Temporal occurrence

Minke whales appear to arrive in the waters of Cape Cod Bay and Massachusetts Bay in the early spring and in some years occurred as late as December. The considerable interannual variability in the abundance of minke whales probably reflects variation in effort (see Table 1) or fluctuations, or both, in the abundance and distribution of prey. That it may be linked to the latter is suggested by the very low sighting rates recorded in 1986 and 1987, two years in which the local abundance of sand lance (*Ammodytes* spp.) is known to have been at a minimum and when other piscivorous mysticetes were largely absent from the study area (Payne et al., 1990). However, the concentration of effort on other mysticetes (and consequently on areas preferred by them) may have introduced a bias against minke whale sightings if these whales exhibit significant differences in habitat preference (this is currently unknown). Interannual variability in abundance has also been reported in other areas and has been similarly linked to prey availability, as well as to effort and, in Arctic areas, distribution of sea ice (Sigurjónsson, 1982; Larsen and Øien, 1988).

There was also considerable variation in abundance from month to month. The data reported here indicate a distinct peak in abundance beginning in July and continuing through September. No minke whales were observed in January or February: although this may have been due to the markedly decreased sampling effort during these two months, this appears unlikely given the dedicated (i.e. non-whale-watching) nature of the surveys conducted at this time and the frequently calm conditions which were a prerequisite for such cruises.

This general pattern of occurrence (abundant in summer, scarce or absent in winter) is similar to that reported for other high-latitude

Table 2

Results (from a one-way analysis of variance) of pairwise comparison of monthly mean sighting rates for minke whales, *Balaenoptera acutorostrata*, in Massachusetts Bay and Cape Cod Bay (1979–92). Figures shown are *P* values; significant differences are shown in bold type.

Month	Apr	May	Jun	Jul	Aug	Sep	Oct
Mar	0.69	0.88	0.98	0.06	0.05	0.06	0.08
Apr		0.64	0.44	**0.01**	**0.01**	**0.01**	**0.02**
May			0.76	**0.01**	**0.01**	**0.01**	**0.02**
Jun				**0.01**	**0.01**	**0.01**	**0.02**
Jul					0.19	0.10	0.13
Aug						0.47	0.58
Sep							0.87

minke whale populations, including those elsewhere in the North Atlantic. Data from Newfoundland, Iceland, and West Greenland show a similar seasonal distribution in which minke whales arrive in spring, are most abundant during mid- to late summer and begin to leave in the autumn (Sergeant, 1963; Mitchell and Kozicki, 1975; Kapel, 1980; Sigurjónsson, 1982). However, a few minke whales have been reported off western Newfoundland and Iceland in both November and December (Sergeant, 1963; Sigurjónsson, 1982), and minke whales have occasionally been caught off West Greenland between November and February (Kapel, 1980). The same seasonal occurrence is seen in the waters off Norway and in the Arctic where a few whales have been observed through the winter (Jonsgård, 1951). High-latitude areas of the North Pacific and the Antarctic are also characterized by a seasonal distribution similar to that observed in the North Atlantic (Shimadzu, 1980; Dorsey, 1983; Gong, 1987; Stern, 1990). Since most of these studies were not based on identified individuals, it is not clear whether minke whales in these areas are resident for long periods or whether the reported sightings represent short-term occupancy or transient passage by numerous animals.

If the apparent decrease in abundance of minke whales in Massachusetts Bay in autumn and winter is, as suggested above, unrelated to effort, it may reflect a migration of most minke whales to lower latitudes at that time of year. Data on the winter distribution of minke whales are scarce. In the southwestern North Atlantic, minke whales have been reported in the waters between Bermuda and the Antilles between the months of January and March (Mitchell, 1991; Mattila and Clapham, 1989; Mattila et al., in press). Stranding data show evidence of the presence of minke whales in the waters off Florida from December to February.[1] Winter sightings, while infrequent, have also been reported in the western Gulf of Maine and in waters southeast of Cape Cod (CeTAP[2]).

In the Southern Hemisphere, minke whales are also reported in lower latitudes during the winter. Off Brazil, as well as in the waters of the southwestern Indian Ocean, minke whales are mainly present in winter and spring (Williamson, 1975; Best, 1982). However, some have been reported trapped in sea ice in the Antarctic between May and October (Taylor, 1957); this finding, together with year-round sightings of minke whales in areas such as California (Stern, 1990), Greenland, Norway, and the Arctic suggests that a few animals may overwinter at higher latitudes.

Calves

During the fourteen years of this study only three minke whale calves were observed. Sightings of minke whale calves in high-latitude areas of the North Atlantic are rare; this is not the case for certain other mysticetes (e.g. humpback whales [Clapham and Mayo, 1987]; fin whales, *Balaenoptera physalus* [Clapham and Seipt, 1991]; North Atlantic right whales [Hamilton and Mayo, 1990]). Only two minke whale calf sightings were reported in the 1982 Cetacean and Turtle Assessment Program (CeTAP) study, both occurring just south of Cape Cod (one in

[1] Mead, J. Curator of marine mammals at the Smithsonian Institution. Natl. Mus. Nat. History, Smithsonian Institution, Washington, D.C. 20560. Unpubl. data, 1992.

[2] CeTAP (Cetacean and Turtle Assessment Program). 1982. Characterization of marine mammals and turtles in the mid- and North Atlantic areas of the U.S. Outer Continental Shelf. Final Rep. of the Cetacean and Turtle Assessment Program, Univ. Rhode Island, to the Bureau of Land Management, Washington, D.C.

April and the other in June). In the waters off Quebec, one pair (adult and calf) was observed in late July (Perkins and Whitehead, 1977). Similarly, calves have not been reported in the waters off the west coast of the United States (Dorsey, 1983) and are also not commonly observed on the high-latitude feeding grounds in the Southern Hemisphere (Kasamatsu et al., 1988).

In the North Atlantic, the majority of minke whale calf sightings have occurred in lower latitudes. In the southwestern North Atlantic, calves have been sighted in the waters between Bermuda and the Antilles (Mitchell, 1991) as well as in the northern Leeward Islands (Mattila and Clapham, 1989).

One possible explanation for the absence of calves in higher latitudes is that minke whales wean their calves before entering these waters. According to Jonsgård (1951), North Atlantic minkes are thought to calve between November and March, and nursing is believed to last for only four to five months. This information would concur with reports of no or few lactating females found during the summer off both Norway (Jonsgård, 1951) and Newfoundland (Sergeant, 1963; Mitchell and Kozicki, 1975).

In the Southern Hemisphere, it also appears that females wean their calves before reaching higher latitudes (Best, 1982; Kato and Miyashita, 1991). However, there is evidence (at least in the Southern Hemisphere) that pairs (mother and calf) may remain in low or middle latitudes until weaning occurs (Kato and Miyashita, 1991), which suggests that some minke whale populations segregate by reproductive class.

Segregation by both sex and age class has been described in many minke whale populations. Whaling data from the North Atlantic, the North Pacific, and the Southern Hemisphere suggest that minke whales segregate by sex during their summer migration (Jonsgård, 1980; Kasamatsu and Ohsumi, 1981; Sigurjónsson, 1982; Larsen and Øien, 1988; Wada, 1989) as well as on their feeding grounds (Jonsgård, 1980; Ohsumi, 1983; Larsen and Øien, 1988; Wada, 1989; Kato et al., 1990a). Segregation by maturational class has also been recorded in minke whales (Best, 1982; Ohsumi, 1983; Wada, 1989; Kato et al., 1990a). Jonsgård (1951) suggested that newly weaned calves and juveniles off Norway probably do not migrate north together with larger animals, which is in agreement with data reported by Wada (1989) for areas off the Pacific coast of Japan.

Neither the sex nor age class of the minke whales in the waters of Cape Cod and Massachusetts Bay areas is known because it is not currently possible to determine either in the field. Stranding data from this area give a mean length for minke whales of 505 cm (n=35, SD=140.3 cm); comparison of this figure with data on lengths of individuals caught in North Atlantic whaling operations (Jonsgård, 1951; Sergeant, 1963; Mitchell and Kozicki, 1975; Christensen, 1981) would suggest that the majority of animals that have stranded here were immature. The sex ratio of stranded animals was approximately even. Whether this sample is representative of the general population or only of those more likely to strand is unknown.

Group size

In this study approximately 95% of all minke whale sightings were singletons. Single animals appear to predominate in other studied areas, although there is evidence of group size changing by season, latitude, sex and age class, and when prey is present. In some cases, however, it is unclear whether animals reported in large groups (particularly when feeding) are actually associated with or are simply attracted to a common location by the presence of prey.

Data from the Mingan Islands in the Gulf of Saint Lawrence show that minke whales are usually solitary, although they are seen in large coordinated groups of five to fifteen animals when actively feeding.[3] Aerial surveys conducted off Iceland in June and July reported a mean school size of 1.1 (Gunnlaugsson et al., 1988). Jonsgård (1951) found that minke whales tend to travel alone off the western coast of Norway, noting only a few sightings consisting of pairs; in the Arctic, single animals were predominant in catches, although groups of three to ten animals were more common than pairs. In the western North Pacific off the Chukotka coast, sightings were usually of single animals. However, when polar cod arrive in late June and in July, minke whales are often observed in groups of five or six animals (Ivashin and Votrogov, 1981); again, it is not clear whether such groups are truly associated according to the definition of 'group' used here. Information on minke whales in the Southern Hemisphere also indicates variabilty in group size with changes in latitude and season as well as with differences in maturational class (Williamson, 1975; Best, 1982; Kato et al., 1989; Kato et al., 1990b).

The group size frequency of minke whales observed in the Massachusetts Bay and Cape Cod Bay areas did not appear to change with time of year or with the presence of prey (on the basis of sightings where confirmed feeding occurred). Because the majority

[3] Sears, R., F. W. Wenzel, and J. M. Williamson. 1981. Behavior and distribution observations of Cetacea along the Quebec north shore (Mingan Islands), summer–fall 1981. Mingan Islands Cetacean Study, Montreal, Unpubl. Rep., 72 p.

of sightings were singletons it is possible that sex or age class has little or no effect on group size in this area, unless one sex or class is disproportionately represented here. The apparent predominance of immature whales among stranded specimens may reflect a similar overrepresentation of juveniles in the general population; if this is the case, the abundance of singletons would agree with the finding of Kato et al. (1990b) that immature animals along with mature males tend to be solitary, whereas mature females usually form schools, especially near the pack ice.

Feeding behavior

In this study less than one percent of all minke whale sightings involved confirmed feeding behavior. The CeTAP study (1982) also reported relatively few sightings of surface feeding. The lack of surface feeding in the study area is odd given that sympatric confamilials are commonly observed feeding (e.g. humpback whales [Payne et al., 1986]; fin whales [Overholtz and Nicolas, 1979]). In other areas of the North Atlantic, minke whales are observed feeding, displaying surface lunges and rolling (Sears et al.[3]; Haycock and Mercer[4]). Near the San Juan Islands, off the west coast of North America, minke whales also exhibit lunging and rolling behavior during feeding (Hoelzel et al., 1989; Dorsey et al., 1990).

Off the San Juan Islands minke whales appear to prey mainly on small schooling fish (juvenile herring, *Clupea harengus*; sand lance, *Ammodytes* spp.) (Dorsey, 1983; Dorsey et al., 1990), which are also the principal food source for minke whales off the Mingan Islands (Sears et al.[3]). Both humpback and fin whales feed primarily on herring or sand lance in the southern Gulf of Maine (Overholtz and Nicolas, 1979; Payne et al., 1990); many observers assume that these fish also represent a principal prey of minke whales, a belief which is strengthened by the scarcity of minke whales in Massachusetts Bay during 1986 and 1987 when the local sand lance population crashed (Payne et al., 1990). However, it is not understood why these minke whales rarely exhibit feeding behavior at the surface, unless whales in this area either exploit fish schools at greater depths than do whales recorded for other feeding grounds or employ a foraging technique that does not utilize the surface for catching prey.

Nearly all minke whales observed feeding during this study were singletons, a finding which is similar to that reported from other areas such as the western coast of North America where minke whales appear to act independently of each other even though several individuals may be present in the same area while feeding (Hoelzel et al., 1989; Dorsey et al., 1990). According to many studies (Ivashin and Votrogov, 1981; Bushuev, 1991, Sears et al.[3]), minke whales tend to group together when food is abundant, but it was unclear whether these animals were feeding cooperatively or were drawn to the same area by the availability of food and were feeding independently.

Conclusion

In general, both the yearly and seasonal distribution of minke whales in Massachusetts Bay and Cape Cod Bay is similar to that found for other populations of this species. The data in this study also generally agree with other published information pertaining to group size, feeding behavior, and the occurrence of mother-and-calf pairs. Unfortunately, because the social structure and group composition of the minke whales observed in this study are unknown, it is impossible to determine whether or not the minke whales of Massachusetts and Cape Cod bays exhibit the same segregational patterns that have been suggested for other populations of this species in both the northern and southern hemispheres. It would also be valuable to explore whether individual minke whales return to the same area from year to year as documented off the west coast of North America, or whether the minke whales seen here represent transient individuals from one or more populations. Continued study with an emphasis on photographic identification of individuals is greatly needed as well as continued work in the biopsy of individuals throughout the year in order to gain some insight on the sex ratio, genetic structure, and group composition of this and other populations.

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[4] Haycock, C. R., and S. N. Mercer. 1984. Observations and notes on the abundance and distribution of cetaceans in the Eastern Bay of Fundy near Brier Island, Nova Scotia, in August and September 1984. Unpubl. Rep.

minkes really are whales and for allowing me extra time to see whether they really do anything besides breathe. This study was made possible in part by funding for data management provided by the U.S. National Marine Fisheries Service (Northeast Fisheries Center) under contract 50-EANF-9-00033.

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Activities of juvenile green turtles, *Chelonia mydas*, at a jettied pass in South Texas

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Green turtles, *Chelonia mydas*, have a worldwide distribution in tropical and subtropical regions. Primary nesting areas in the Atlantic region are located at Ascension Island, Aves Island, Costa Rica, and Surinam. The east coast of Florida has the largest breeding assemblage in the United States. The species is listed as endangered by the International Union for the Conservation of Nature (IUCN) (Groombridge, 1982) and is listed as threatened in all areas, except for breeding populations in Florida and the Pacific coast of Mexico, which are listed as endangered (National Marine Fisheries Service, 1991).

During most of the nineteenth century, green turtles were abundant throughout Texas, including the lower Laguna Madre (Hildebrand, 1982; Doughty, 1984). Commercial harvest of these turtles peaked in 1890; Texas landings increased to about 2,160 turtles (265,000 kg) from an estimated 89 turtles (10,909 kg) in 1880. By the early twentieth century the fishery had collapsed (Doughty, 1984).

Understanding habitat needs has been recognized as an essential element for successful recovery of sea turtle stocks in the Gulf of Mexico (Thompson et al., 1990). Distribution, movements, and feeding habits of pelagic hatchlings are unknown. Little research has been conducted on sea turtle populations in Texas. Published stranding data suggest that Texas nearshore and inshore waters are important habitats for juvenile and subadult sea turtles (Rabalais and Rabalais, 1980; Manzella and Williams, 1992). Recent tracking and mark-recapture studies on green turtles indicate that jetties and channel entrances along the south Texas coast serve as summer developmental habitats for this species[1,2] (Manzella et al., 1990; Shaver, 1990, 1994). This is supported by higher numbers of sightings in south Texas versus the upper Texas and west Louisiana coasts (Williams and Manzella, 1991).

Turtles using jetties and channel entrances could interact with human activities, such as channel dredging, shrimping, and recreational fishing and boating. The level of such interaction is dependent on the nature and degree of jetty and channel utilization. Studies conducted during 1991[1,2] indicated that green turtles may utilize jetty habitat to a greater degree than other habitats within Brazos-Santiago Pass, on the basis of sightings and the behavior of a single radio-tracked turtle. The objectives of our study were to describe juvenile green turtle movements within Brazos-Santiago Pass, Texas. We hypothesized that juvenile green turtles select jetty habitat over other habitats within Brazos-Santiago Pass.

Materials and methods

Study area

The study was conducted in the Brazos Santiago Pass area, South Padre Island, Texas (Fig. 1). The pass, extending from the tip of the jetties to the western edge of Barracuda and Dolphin Coves, links the Laguna Madre to the Gulf of Mexico. Landry et al.[1] characterized habitat types within the pass. Using their data, we designated four habitats in the pass area.

The jetty habitat extended 10 m from the visible jetty, with water depths up to 3 m. It contained partially exposed and submerged granite boulders and rubble, which decreased in density as distance from the jetty increased. The highest density and concentration of sessile organisms were found in this habitat. Barnacles (*Balanus* sp.), sea urchins (*Arbacia punctulata*), and

[1] Landry, A., Jr., D. Costa, B. Williams, and M. Coyne. 1992. Turtle capture and habitat characterization study. Final Rep. submitted to the U.S. Army Corps of Engineers, Galveston District, 2000 Fort Point Blvd., Galveston, TX 77553, 112 p.

[2] Renaud, M., G. Gitschlag, E. Klima, S. Manzella, and J. Williams. 1992. Tracking of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles using radio and sonic telemetry at South Padre Island, Texas. June–September 1991. Final Rep. to the U.S. Army Corps of Engineers, Galveston District, 2000 Fort Point Blvd., Galveston, TX 77553, 52 p.

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Fishery Bulletin 93:586–593 (1995).

three algal species (*Ulva fasciata*, *Podina vickersiae*, and *Bryocladia thysigera*), were the most abundant organisms associated with jetty structure.[1] The near-jetty habitat encompassed areas of barren bottom and scattered boulders on both the Gulf and pass side of the jetty. Channel habitat, the dredged portion of the Brownsville Ship Channel between the jetties, extended seaward from Barracuda and Dolphin Coves to the tip of the jetties. It was characterized by a scoured bottom, nearly void of vegetation. Water depths ranged from 10 to 15.2 m and averaged 12.5 m. Channel width was about 90 m for most of its length. East of the coves, the distance from the jetty to the channel edge ranged from 115 to 152 m. Barren rippled sand, water depths up to 7.5 m, and few organisms were noted within the cove habitat.

Capture of sea turtles

Turtles were obtained from Texas A&M University (TAMU) Institute of Marine Life Science personnel, who were conducting a netting and habitat characterization study at Brazos-Santiago Pass.[3] Turtles were captured either through use of entanglement nets (45.7–91.5 m long, 3.7–7.3 m deep, 12.7 cm bar mesh) set at the Gulf side of the South Jetty, or by encircling a targeted turtle in the shallow coves with the entanglement net. For turtles exhibiting strong site fidelity, 1-m diameter cast nets were used for some captures along the jetties.

Tagging activities

Following capture, turtles were transported 1–2 km to a holding facility where they were kept for 24–48 hours. We recorded turtle weights, straight and curved carapace lengths and widths, and applied radio and sonic transmitters. Telonics radio transmitters (180 g) with 40-cm antennas were fitted with fiberglass to the second neural scute of nine turtles, and Sonotronics sonic transmitters (36 g) were bolted to the posterior marginal scutes. Turtles were designated T1 through T9. The weight of the backpack-type transmitters never exceeded

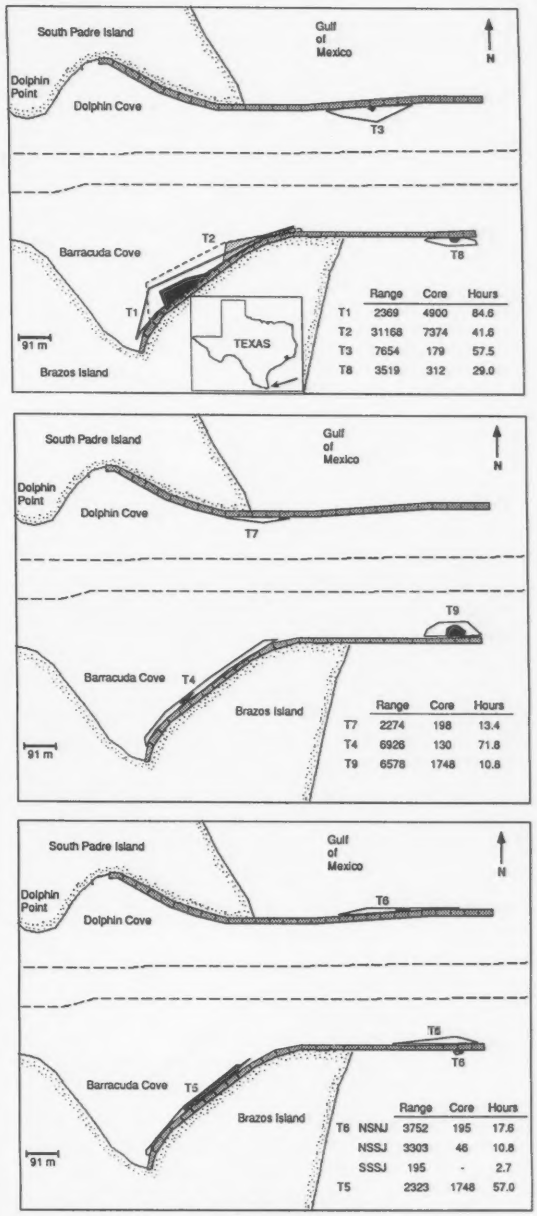

Figure 1

Range (m^2), core area (m^2), and total hours tracked for individual green turtles, *Chelonia mydas*, T1-T9, during August–September 1992. Core area is displayed in solid black and range is enclosed by a solid line for all turtles except T2. T2 has a shaded area representing its core area and a dashed line surrounding its range. For T6, NSNJ = north side of north jetty, NSSJ = north side of south jetty, and SSSJ = south side of south jetty. An inset of the state of Texas with an arrow showing our area of study is located in the upper third of the figure.

[3] Landry, A., Jr., D. Costa, M. Coyne, K. St. John, and B. Williams. 1993. Sea turtle capture and habitat characterization: South Padre Island and Sabine Pass, TX environs. Final Rep. submitted to the U.S. Army Corps of Engineers, Galveston District, 2000 Fort Point Blvd., Galveston, TX 77553, 109 p.

10% of the weight of the turtle, in accordance with the safety recommendations of Brander and Cochran (1969), Bradbury et al. (1979), Aldridge and Bringham (1988), and Byles and Keinath (1990).

Tracking

Turtles were released at their capture sites between 0900 and 1600 hours. We used a Telonics TR2/TS1 receiver-scanner connected to a directional 5-element Yagi antenna to monitor radio transmitters until they became detached from turtles. Maximum radius of signal reception with this equipment is approximately 16 km. When weather prohibited tracking by vessel, turtles were monitored from land. Sonic transmitters were monitored by using a Dukane directional hydrophone with a receiving range between 0.6 and 1.1 km. Sonic tracking alone was used when a turtle had lost its radio transmitter but retained its sonic transmitter or when a second turtle was present in the area of a turtle being monitored by radio.

Data were collected for 12 hours each day. All hours of the day and night were included by offsetting each day's start time by two hours from that of the previous day. We attempted daily to locate every turtle with a functioning transmitter. Up to five turtles were tracked during each day. Geographic location was recorded when a turtle was sighted or its position obtained with sonic telemetry. Reference marks were painted at 50-m intervals on jetty boulders, westward from the seaward tip of each jetty. Locations of turtles were determined with respect to reference marks and to visual estimates of perpendicular distance from the jetties. When possible, turtle locations >40 m from the jetty were recorded by means of a portable global positioning system. The total time spent between jetty reference marks was calculated for each turtle. Each turtle position was given a weight equal to time spent at that position. These weighted positions were then used to calculate a mean position for each turtle. Minimum observation time used for this analysis was 5 minutes. Range (area containing 95% of locations) and core area (area containing 50% of locations) were developed by using the minimum convex polygon method (Mohr, 1947), modified to exclude nonwater areas. To discern differences in movement patterns, the ranges and core areas for each turtle were determined for dawn (0500–0900 h), day (0900–1700 h), dusk (1700–2100 h), and night (2100–0500 h) if at least three days were sampled and >5 h of tracking information were available for a turtle within a time period. To obtain an index of turtle movements, the distance and time between surfacing events were calculated for each turtle and used to estimate mean speed of movements for dawn, day, dusk, night, and all times combined.

Surface and submergence behavior

Surface and submergence times were calculated for each turtle affixed with a radio transmitter. Data collected on the day of release were omitted from analyses of ranges and of surface or submergence behaviors. Surface time was considered to be the interval between the beginning and ending of radio signals (i.e. when the turtle was within 40 cm of the ocean surface). Submergence time was defined as the interval between the end of a radio signal and the beginning of the next signal (i.e. when the turtle was deeper than 40 cm). Overall mean surface and submergence times, and day, night, dawn, and dusk means were calculated for each turtle. A surface or submergence interval overlapping two time periods was included in the period containing the majority of the interval.

Statistical methods

Distribution of variables (surface and submergence times, movement speed) were tested with the Shapiro-Wilk test for normality (α=0.05). The Kruskall-Wallis analysis was used to test for differences in means between dawn, day, dusk, and night (α=0.05) (Sokal and Rohlf, 1981) when the null hypothesis (normal distribution) was rejected. If a significant difference was indicated, a means test described by Conover (1980) was used to determine which means differed, again by using α=0.05.

Results

Sea turtle movement patterns

Nine green turtles (29.1–47.9 cm straight carapace length [SCL], 2.6–14.8 kg) were tracked from 14 to 58 days from 31 July to 26 September 1992 (Table 1). Differences in tracking periods were due to different capture dates and variable tag retention. In addition, on some days certain turtles could not be located owing to inclement weather. All turtles moved away from the jetties immediately following release. Those released between the jetties entered the deeper waters of the channel, but T8, released on the Gulf side of the south jetty, moved south, roughly parallel to the beach. Seven turtles returned to the jetties within an hour. T6 and T7 went offshore after entering the channel and returned to the jetties the next

Table 1

Percent total submergence time (PTST), maximum submergence time (MST, minutes), weight (kg), straight carapace length (SCL, cm), and dates tracked for nine green turtles, *Chelonia mydas*, at South Padre Island, Texas.

Turtle	PTST	MST	Weight	SCL	Date
T1	88.8	24.3	14.8	47.9	31 Jul –26 Sep
T2	92.4	21.4	11.5	44.7	01 Aug–25 Sep
T3	96.3	32.9	3.1	30.1	01 Aug–26 Sep
T4	80.8	31.2	2.7	29.1	01 Aug–26 Sep
T5	90.1	25.4	2.6	29.2	01 Aug–26 Sep
T6	96.3	39.8	3.6	31.5	02 Aug–26 Sep
T7	93.1	25.8	3.9	33.3	06 Aug–26 Sep
T8	96.5	37.8	3.4	31.5	09 Aug–26 Sep
T9	97.8	38.1	4.1	33.0	10 Aug–23 Sep

day. Seven turtles remained in the general area of their capture throughout the study period. Of the others, T6 used three areas along both jetties and T7 moved extensively along both jetties before moving up the channel and into South Bay. Only data from the pass were used in analyses for T7.

Daily movements of turtles along the jetties ranged from less than 50 m to more than 1,000 m. Mean rate of movement ranged from 8 m/h to 568 m/h (Table 2). The least movement occurred at night, ranging from 8–127 m/h. Seventy percent of all locations were within 5 m of the jetties. Only 0.3% were within channel boundaries, including five channel crossings. Overall areal ranges of turtles remaining in the jetty area were from 2,274 to 31,168 m^2. Overall core areas ranged from 130 to 7,374 m^2.

Five of the nine turtles tracked had ranges restricted to the north side of the south jetty (Fig. 1). Northerly winds, in excess of 20 knots, coincided with the movement of T6 from the windward side of the north jetty into protected waters near the south jetty by day 14. Mean locations for three turtles (T1, T4, and T5) were within 400 m of the Barracuda Cove beach. The mean location of T2 was about 650 m from the beach, about halfway up the jetty. The only turtle that had significantly different mean locations for different time periods was T1 ($P<0.05$). The mean dusk location of T1 was about 250 m closer to the jetty tip than its mean dawn and day locations and over 400 m closer than its mean night location. T3, on the south side of the north jetty, also showed greater westward movement at night than at any other time ($P<0.05$).

Table 2

Mean distance (m) moved by hour by time period for nine green turtles, *Chelonia mydas*, tracked near South Padre Island, Texas. A line above mean movements indicates no significant difference ($\alpha=0.05$).

Turtle	Time of day			
T1 Period	Night	Dawn	Dusk	Day
Mean distance	127	161	401	251
T2 Period	Night	Dawn	Day	Dusk
Mean distance	8	148	440	568
T3 Period	Dusk	Day	Dawn	
Mean distance	20	102	323	
T4 Period	Night	Dusk	Dawn	Day
Mean distance	25	223	243	330
T5 Period	Night	Day	Dawn	Dusk
Mean distance	45	144	108	191
T6 Period	Dusk	Day		
Mean distance	59	225		
T7 Period	Night	Dawn	Day	
Mean distance	9	496	517	
T8 Period	Dawn	Dusk	Day	
Mean distance	171	195	201	
T9 Period	Day	Dawn		
Mean distance	114	149		

Submergence and surface behavior

Tracking was conducted for a total of 108 hours at dawn, 247 h during the day, 60 h at dusk, and 151 h at night. Time spent submerged ranged from 80.8 to 97.8% and averaged 91% for all turtles (Table 1). Submergence time ranged from 0.02 to 39.8 minutes. Overall mean submergence time varied from 1.9 to 6.1 min between turtles. Surface time ranged from 1 to 1,146 seconds. Overall mean surface time varied from 8.5 to 26.5 seconds.

A breakdown of submergence time by turtle revealed that 99% of all turtle submergences were <20 min, 74–96% were <10 min, and 38–64% were <1 min (Fig. 2). Submergence patterns were significantly different when data were analyzed by dawn, day, dusk, and night (Table 3). The number of submergences >10 min was higher at night than at other time periods for every turtle tracked at night.

A breakdown of surface time by turtle revealed that 99% of all turtle surfacings were <120 sec, 67–92% were <15 sec, and 41–77% were <5 sec (Fig. 2). Surface patterns also were significantly different when

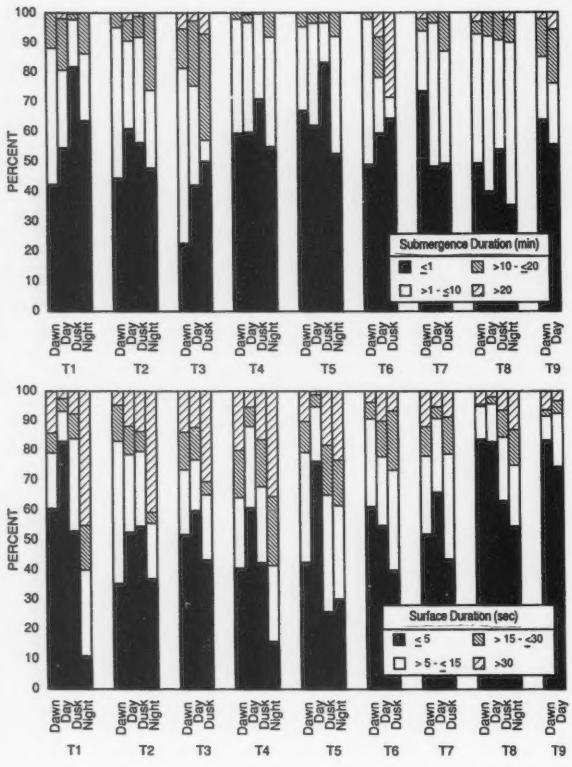

Figure 2

Green turtle, *Chelonia mydas*, submergence and surface durations by specified time intervals in hours, dawn (0500–0900), day (0900–1700), dusk (1700–2100), and night (2100–0500).

data were analyzed by dawn, day, dusk, and night (Table 3). The number of surfacings >15 sec was higher at night than at other periods for every turtle tracked at night. The mean surface time was significantly higher at night than at all other time periods for four of six turtles tracked at night.

Discussion

Movements and habitat use

Habitat use by juvenile green turtles in the Brazos-Santiago Pass was not proportional to available habitat.[1,2] The jetty habitat, which contained extensive algal mats, received a disproportionately high amount of use, suggesting that turtles possibly congregated there for food. Analysis of stomach contents of juvenile green turtles by Landry et al.[3] support the utilization of algal food sources. Turtles in this study were seen feeding on algal growth along the jetties, especially at dusk. The abundance of food may account for the high site fidelity and small core areas. Other studies of similar-size green turtles described their food source as algae (Wershoven and Wershoven, 1989; Wershoven and Wershoven, 1991), both algae and sea grasses (Burke et al., 1991), and primarily sea grasses (Ogden et al., 1983). Mendonca (1983), working with larger turtles (7.8–54.5 kg) postulated that green turtles prefer sea grass. Sea grasses were present within 1 km of the jetty habitat of our study area.[4] One turtle from our study entered and remained in a sea grass habitat for over a month; however, no fecal or stomach samples were taken while it was in this habitat. Bjorndal et al. (1991) suggested that green turtles possess gut microflora for digestion of both algae and seagrass and that the relative abundance of microbial species would vary in response to longterm changes in diet. Therefore, turtles could take advantage of a local abundance in either food source.

All of the turtles in this study had small ranges of movement. A juvenile green turtle tracked at the jetties in 1991 also showed limited movements.[2] The most limited movements were at night, suggesting that resting was most common at night. This hypothesis is supported in studies by Bjorndal (1980), Mendonca (1983), and Ogden et al. (1983) who documented resting areas for turtles at night coupled with a shorter range of movements compared with activity during the day. Mendonca (1983) noted that during summer months the resting sites of green turtles on consecutive nights were within meters of the previous night's rest site. The reason for the westward movements of T1 at night is unknown. The more sheltered jetty habitat adjacent to the cove may have been preferred for resting at night, whereas a broader stretch of the jetty was utilized for daytime foraging activities. Turtles at the jetties apparently have an abundant food source in proximity to resting sites. In contrast, Mendonca (1983) recorded areal ranges of 0.48 to

[4] Quammen, M., and C. Onuf. 1991. Laguna Madre: seagrass changes continue decades after salinity reduction. Rep. to the National Wetlands Center, U.S. Fish Wildl. Serv., Campus Box 39, 6300 Ocean Dr., Corpus Christi, TX 78412, 27 p.

5.06 km^2 for juvenile green turtles. Ogden et al. (1983) found turtles moved up to 0.5 km between feeding and resting sites, but they did not report ranges of movement.

Turtles appeared to select for the south jetty. Landry et al.[3] also recorded many more turtle sightings at the south jetty than at the north jetty. Of two turtles caught at the north jetty, only one remained there longer than two weeks. The other moved to the south jetty during northerly winds in excess of 20 knots. Because of its accessibility, the north jetty received much more use by the public than the south jetty. The effect of this disproportionate use on turtle presence or behavior, or both, during the study is unknown.

Submergence behavior

Green turtle behavior was characterized by numerous short submergences and surfacings. Submergences ≤5 min occurred mostly during dusk and dawn when active periods of foraging were observed. We felt this was a direct effect of the shallow habitat occupied by the turtles. The transmitter antenna could be exposed at times when the turtle was still submerged. Submergence ≥10 min was observed at night and minimally during the afternoon.

Submergence durations by green turtles in our study was similar to that for green turtles studied by Renaud et al.[2] Eighty-nine to ninety-nine percent of the submergences were <10 min in duration and 17–56% were <1 minute. Mean submergence times for turtles in our study were considerably shorter than the mean submergence times of Kemp's ridleys found by Byles (1989) (18.1 min), and Mendonca and Pritchard (1986) (16.7 min). This may be a result of the different habitats and feeding behaviors of Kemp's ridleys and the green turtles in our study. Our turtles also were smaller than turtles in the other two studies.

The percentage of submerged time for each 24-h day ranged from 80.8–97.8%. The turtles with the three lowest percent submerged times were observed for long periods with their antenna only partially exposed. This behavior undoubtedly lowered their submerged to surface ratio. Balazs (1994), through satellite telemetry, found that two migrating adult green turtles in the Pacific Ocean spent 95–96% of their time submerged. Renaud and Carpenter (1994) found percent submerged time to be 90.0–95.7% for three satellite-tracked juvenile loggerhead turtles, *Caretta caretta*, in the Gulf of Mexico. Two satellite-tracked juvenile Kemp's ridley sea turtles, in the Atlantic and Gulf of Mexico, had percent submerged times of 94.0–98.6% (Renaud, in press). Byles (1989), studying adult Kemp's ridleys in the Gulf of Mexico with satellite telemetry, found that they spent an average 96% of the time submerged. A study of radio-tracked loggerheads with 64.0–91.9 cm carapace length (straight or curved not specified) in the Canaveral Channel, Florida, revealed that they averaged 96.2% of the time submerged (Kemmerer et al., 1983).

Table 3

Mean surface and submergence times (nearest sec) by time period, for nine green turtles, *Chelonia mydas*, tracked near South Padre Island, Texas. A line above mean values indicates no significant difference (α=0.05). D = day; K = dusk; N = night; W = dawn.

Turtle		Time of day			
T1	Surface	D5	K11	W13	N47
	Submerge	K60	N172	W214	D236
T2	Surface	D15	K21	W10	N26
	Submerge	D142	K143	W153	N320
T3	Surface	D12	W13	K16	N56
	Submerge	D327	W366	K446	N1371
T4	Surface	D19	K24	W29	N35
	Submerge	K58	D102	W108	N169
T5	Surface	D5	W13	K19	N20
	Submerge	K70	D102	W109	N187
T6	Surface	W7	D11	K15	N80
	Submerge	W125	D321	K501	
T7	Surface	D9	K12	W14	
	Submerge	W123	D145	K184	
T8	Surface	D5	W6	K9	N13
	Submerge	K171	D174	W175	N258
T9	Surface	W6	D6		
	Submerge	W212	D313		

Channel use

During our study, turtles remained primarily near the jetties, probably because food was abundant there and virtually absent in the channel and barren bottom areas. Turtles were found in the channel <0.3% of the time. They appeared to use the channel for transit to other areas or as presumed escape cover.

Conclusions

Our data, combined with numerous sightings of turtles at the jetty[3] and with the fact that there was no appreciable movement away from the jetties by tracked turtles, support the hypothesis that juvenile green turtles in Brazos-Santiago Pass, south Texas, selected for jetty habitat over other habitats available. If this pattern is consistent for all times that green turtles inhabit the pass, then it would indicate that potential harm from hopper dredging or channel boat traffic would be minimal. Our study included only nine turtles and was limited to August–September 1992. Therefore, caution should be used in extrapolating our results to other years or times of the year. The study was timed to coincide with the period of highest turtle abundance in the pass. Data gathered by TAMU indicate that use of the pass by green turtles increases during June–September.[1,3] Turtles appear to be rare from December to March and gradually begin to increase in numbers starting in April. We were unable to monitor turtle behavior during dredging, because no dredging was done during the study; therefore, we do not know how dredging of the channel may affect behavior of turtles occupying the jetty habitat.

Because green turtles are herbivorous, there is very little danger of hook and line captures from jetty fishing. The greatest impact on turtle behavior may be simply that of human activity on the jetties. The level of that impact is currently unknown. We encourage further study, particularly during other times of the year.

Acknowledgments

We would like to acknowledge several organizations and their personnel for assistance in making this work possible: the U.S. Army Corps of Engineers (Galveston and New Orleans Districts) for funding the research, Texas A&M University for capturing sea turtles and characterizing habitats in the lower Laguna Madre, the University of Texas Pan American Coastal Studies Laboratory for making their facility available to hold turtles, and the U.S. Coast Guard Station at South Padre Island for use of their base to store our tracking vessel. Special thanks go to Gregg Gitschlag for development of the turtle monitoring system along the jetties.

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Determination of age and growth of swordfish, *Xiphias gladius* L., 1758, in the eastern Mediterranean using anal-fin spines

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Estimates of growth rates of billfish are important because they are necessary elements of population dynamics models used in the assessment of stocks for this family of fish. Otoliths have been used for ageing most billfish species (Radtke, 1983; Radtke and Hurley, 1983; Wilson and Dean, 1983; Prince et al., 1984; Hill et al., 1989) but several authors have pointed out that the use of dorsal- and anal-fin spines are more practical in terms of ease of collection and processing (Berkeley and Houde, 1983; Hedgepeth and Jolley, 1983; Hill et al., 1989; Tsimenides and Tserpes, 1989). Other skeletal structures such as vertebrae have rarely been used and results have been poor (Prince et al., 1984; Hill et al., 1989).

The swordfish, *Xiphias gladius*, is a cosmopolitan billfish species that is highly exploited in the Atlantic Ocean and the Mediterranean Sea. In the Mediterranean the average size of harvested swordfish has declined over the last decade such that juveniles compose as much as 50–80% of the catch (Di Natale, 1990; Tserpes et al., 1993). However, the existence of contradictory estimates of growth parameters makes assessment of swordfish stocks difficult (Anonymous, 1990; 1993).

Age of swordfish has been estimated from otoliths (Radtke and Hurley, 1983; Wilson and Dean, 1983), and sections of anal-fin spines (Berkeley and Houde, 1983). Of these ageing methods only Ehrhardt (1992) achieved partial validation of the anal-fin method through marginal increment analysis. This analysis assumes that time of annulus formation corresponds to the time when marginal increments are minimal, and it has been widely used to determine the timing of annual increment formation in otoliths and scales of various fish species (Wenner et al., 1986; Maceina et al., 1987). Although the assumption of the analysis is valid for any ageing structure, the method has rarely been applied to structures other than otoliths and scales.

Tsimenides and Tserpes (1989) conducted growth studies on swordfish from the Aegean sea using anal-fin spines but did not attempt validation. They concluded that there was "a degree of uncertainty" in age estimates due to the loss of the first annulus in older animals.

The primary goal of this paper is to determine whether growth bands in anal-fin spines used for age determination of swordfish are deposited annually. Because Ehrhardt (1992) reported that the von Bertalanffy growth function did not adequately represent swordfish growth, we propose a second objective, namely to compare the growth function proposed by Ehrhardt (1992) with the standard von Bertalanffy model for representing growth of Mediterranean swordfish.

Materials and methods

Fish sampling and spine preparation

A total of 1,325 swordfish samples were obtained from commercial longline catches landed at the ports of Kalimnos (n=782), Kithnos (n=185), and Chania (n=358) in the Aegean sea. These ports, located on the islands of Kalimnos, Kithnos, and Crete are part of a national project addressing the fishery and biology of swordfish in the Greek seas (De Metrio et al., 1989). Samples were collected from 1987 to 1992 during alternate months from February to October. However, most were collected from May to September when the majority of catches occur.

Measurements of lower-jaw fork length (LJFL to nearest cm) were taken for all fish, sex was determined, and the anal fin removed and frozen for storage. In the laboratory, fins were thawed and sections of the second spine of the anal fin were prepared for reading according to the method described by Tsimenides and Tserpes (1989). Specifically, each anal fin was immersed in boiling water for a few minutes before the second spine was removed, freed from skin and tissue, cleaned with water, and left

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to dry completely. A section about 2 cm thick was cut with an electric saw from each dried spine at the point where the spine flares (condyle). Each section was placed in a plastic cylinder (3 cm diameter and 2 cm height) which was then filled with liquid resin. These were left to dry for at least 12 hours, the plastic case was removed, and two or three sections about 1 mm thick were cut distally with a "Stuers" accutom.

Age determination

Spine sections were read under a binocular microscope at 12× magnification by using reflected light and a dark background. The distances from the focus to the edge of the section on the dorsal rim (spine radius) and from the focus to each annulus were measured with an optical micrometer. Sections were read by two readers and identical counts were obtained in >80% of the cases; samples were considered unreadable and were excluded from the analysis if discrepancies in counts could not be resolved.

Typically, broad opaque bands and narrow translucent ones could be seen alternating outwards from the central core. Translucent bands that form around the entire circumference of the spine were considered to be annuli and the total number of these bands was recorded (Fig. 1).

Age classes were assigned on the basis of the number of annuli and the following characteristics of the bands: 1) the disappearance of the first annulus from older fish and 2) the existence of multiple bands mainly in larger fish. Preliminary analysis of LJFL measurements taken in nursery areas of the Aegean sea have shown that swordfish reach a length of about 80–90 cm at one year of age. The first annulus could be seen in fish of this size at an average distance of 1.5 mm (SD=0.08) from the focus, but it was usually not visible at lengths greater than 100 cm (Fig. 1). In such cases, and if the total spine radius was greater than 1.5 mm, one year was added to the assigned age. As described by Berkeley and Houde (1983), multiple bands are those which form around the entire circumference of the spine such that the distance between them is substantially less than that of the preceding and following annual bands. In these cases, the clearest band was considered an annulus and the others were ignored. However, if it was not possible to identify such a band, the specimen was considered unreadable. When the opaque-translucent zonation was such that annuli could not be defined, such specimens were also considered unreadable.

Data analysis

The marginal increment ratio (MIR) was estimated for each specimen according to the formula:

$$MIR = (S - r_n) / S,$$

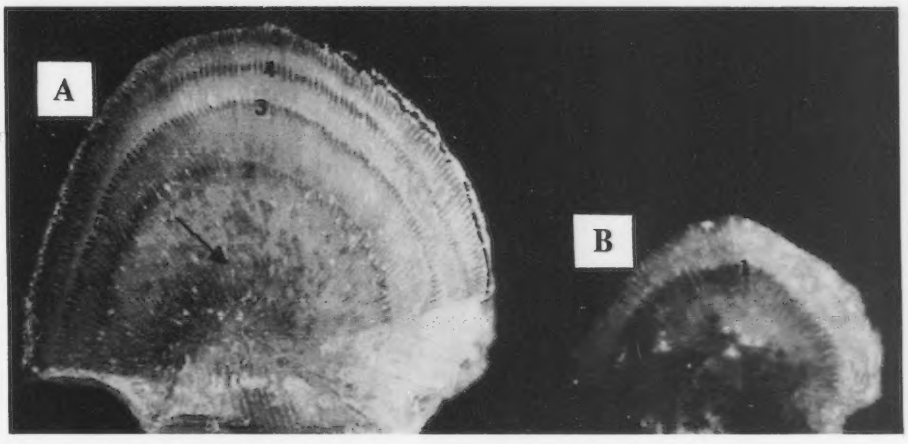

Figure 1

Sections of second anal-fin spine with five growth zones (**A**) and one growth zone (**B**) used for age determination of swordfish, *Xiphias gladius*, from the eastern Mediterranean. First annulus is missing in section (A) whereas it can be clearly seen in section (B). Estimated location of first annulus in section (A), based on its location in section (B), is indicated by an arrow. Lower-jaw fork lengths (LJFL) of animals (A) and (B) were 162 and 95 cm, respectively.

where S = spine radius; and
r_n = radius of the most recent annulus.

The mean *MIR* and the standard deviation were computed for each month and age separately. Marginal increment analysis was not performed for age 1 because the first annulus was usually missing, nor for ages greater than 5 because of a lack of sufficient number of samples.

Estimates of theoretical growth in length were obtained by fitting mean monthly length-at-age data to two forms of the von Bertalanffy growth equation: 1) the standard form and 2) the generalized form as proposed by Chapman (1961).

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \quad (1)$$

$$L_t = \left[L_\infty^{(1-\delta)} - \left(L_\infty^{(1-\delta)} - l_0^{(1-\delta)}\right) e^{-k(1-\delta)t}\right]^{1/(1-\delta)} \quad (2)$$

where L_t = LJFL at age t, L = asymptotic length, k = growth coefficient, t_0 = theoretical age at zero length, l_0 = length at zero age, and δ = fitted fourth function parameter.

Mean data were used in order to assign equal weight to all observations. Only mean values from samples of greater than five fish were used. Growth parameters of both models were estimated iteratively by using the Simplex minimization algorithm (Wilkinson, 1988). The measure of goodness of fit was the coefficient of determination (r^2). Date of birth was set at 1 June because swordfish spawn in the Mediterranean sea in early summer (Palco et al., 1981).

Growth parameters were estimated for males, females, and sexes combined, and sex differences were tested by analysis of the residual sum of squares (ARSS) as suggested by Chen et al. (1992). This method is a modification of the ARSS originally developed for the comparison of linear models (Zar, 1984).

Back calculations of length at age were estimated in two ways.

1 From a modified version of the direct proportion formula (Fraser, 1916; Lee, 1920):

$$L_n - c = (S_n / S)(L - c),$$

where L_n = LJFL when the annulus n was formed;
L = LJFL at time of capture;
c = intercept on length axis from linear regression of length on spine radius;
S_n = distance from spine focus to annulus n; and
S = spine radius.

2 From the formula of Monastyrsky (Bagenal and Tesch, 1978):

$$L_n = (S_n / S)^b L$$

where L_n = LJFL when the annulus n was formed;
L = LJFL at time of capture;
b = the exponent of the regression of length (L) on spine radius (S) which is assumed to be a power function of the form $L=aS^b$;
S_n = distance from spine focus to annulus n; and
S = spine radius.

The constant b was calculated from the logarithmic form of the power function.

In both cases the relation between spine radius and LJFL was determined for males and females and for sexes combined. Moreover, the regression lines for males and females were tested for equality of slopes and if significant differences were found, intercepts were tested by means of analysis of covariance (Dixon and Massey, 1985). No back calculations were attempted for age one because the first annulus was missing in the vast majority of the specimens. All statistical inferences were based on the 0.05 significance level.

Results

Of the 1,325 swordfish sampled, 1,100 were aged successfully (521 males and 579 females). The lengths of individuals ranged from 62 to 210 cm (Fig. 2). In 64 of the 225 unreadable spines, no annuli could be identified because the opaque-translucent zonation was unclear. The remaining 161 spines were considered unreadable owing to the existence of multiple bands which made the identification of annuli difficult or which resulted in ageing discrepancies between the readers, or both.

Up to 9 rings, assumed to be annuli, were visible in the anal-fin spines sampled. Sample sizes for all age classes were greater than 20, except for class 9 (15). Two-year-old fish were the dominant age class and over 80% of the fish were less than 5 years old. Differences in mean size between the successive age classes were calculated to reveal any peculiarities in growth patterns. In theory, absolute growth was expected to be rapid at first and to decrease progressively in later life. The pattern observed for swordfish generally agreed with these expectations (Table 1). Monthly means of MIR indicated that an annu-

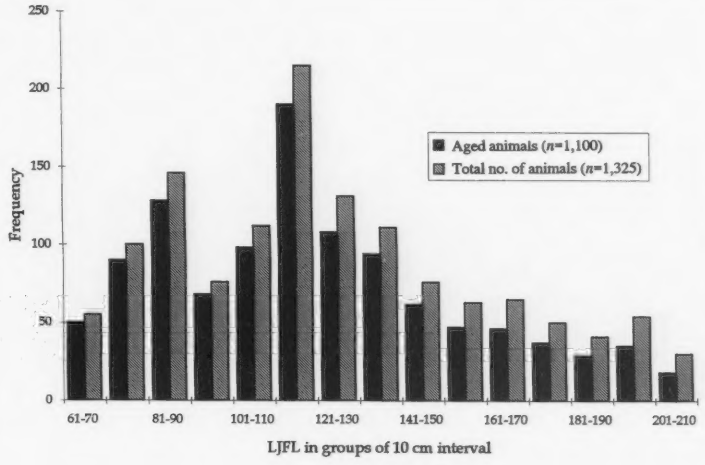

Figure 2

Length-frequency distribution of swordfish, *Xiphias gladius*, from the eastern Mediterranean indicating the total number of fish and the number of those with readable spines (aged animals). LJFL = lower-jaw fork length, n = sample size.

lus is formed from middle spring to early summer for all ages examined (Fig. 3).

Parameters of the standard von Bertalanffy growth function and the generalized model were computed for males, females, and sexes combined (Tables 2). Both models provided a good fit to the data (Fig. 4). Results of the ARSS revealed that growth differences between sexes were always highly significant (F=8.22, P<0.001 for the standard growth function; F=7.41, P<0.001 for the generalized model).

The intercept values used in the proportional formula of back calculation were obtained from the linear regression of LJFL on spine radius:

$LJFL = 59.09 + 18.32(S)$ [r^2=0.98 for males];
$LJFL = 62.43 + 17.02(S)$ [r^2=0.98 for females]; and
$LJFL = 61.45 + 17.39(S)$ [r^2=0.98 for both sexes combined],

where $LJFL$ = lower-jaw fork length (cm);
S = anal-fin spine radius (mm); and
r^2 = coefficient of determination.

Males and females had significantly different slopes (F=44.85, P<0.001).

The constant b used for the nonlinear method of back calculation was obtained from the slope values of the relation between $LJFL$ and spine radius:

Table 1

Summary statistics on sizes of aged swordfish, *Xiphias gladius*, from the eastern Mediterranean. LJFL = lower-jaw fork length.

Age	Sample size	Mean LJFL (cm)	Standard error	LJFL range (cm)	Mean size increment
0	128	72.59	0.51	62–88	—
1	232	89.71	0.52	75–115	—
2	326	114.90	0.33	102–130	25.19
3	153	134.20	0.59	119–153	19.30
4	84	150.46	0.97	126–169	16.26
5	48	162.35	1.04	148–176	11.89
6	54	174.37	0.93	159–185	12.02
7	27	186.81	1.11	179–199	12.44
8	33	198.27	1.13	190–210	11.46
9	15	199.40	1.09	193–205	1.13

$\ln(LJFL) = 4.30 + 0.43(\ln S)$ [r^2=0.94 for males];
$\ln(LJFL) = 4.30 + 0.44(\ln S)$ [r^2=0.96 for females]; and
$\ln(LJFL) = 4.30 + 0.44(\ln S)$ [r^2=0.96 for both sexes combined].

The slope of the relationship differed significantly between males and females (F=6.33, P=0.01).

The statistically significant differences between the sexes for the LJFL spine-radius relation are likely

Table 2

Parameter estimates for the standard von Bertalanffy and the generalized von Bertalanffy growth model for swordfish, *Xiphias gladius*, from the eastern Mediterranean. Corresponding r^2 values are shown in parenthesis. See text for parameter definitions.

	Standard von Bertalanffy			Generalized von Bertalanffy		
Parameter	Male (r^2=0.99)	Female (r^2=0.99)	Sexes combined (r^2=0.99)	Male (r^2=0.99)	Female (r^2=0.99)	Sexes combined (r^2=0.99)
L_∞	203.076	226.525	238.582	292.967	274.914	385.503
k	0.241	0.210	0.185	0.020	0.037	0.011
t_0	−1.205	−1.165	−1.404			
l_0				0.000	0.000	0.002
δ				−1.434	−1.140	−1.393

due to the small variance of the recorded values rather than to a morphometric discrimination between sexes. This can be seen by solving the equations for different spine-radius values. For example, the computed LJFL values for a spine radius of 2 mm are: 1) 95.73 for males and 96.47 cm for females from the linear method; and 2) 99.29 for males and 99.98 for females from the nonlinear method.

The LJFL at the end of each year of life was backcalculated for each individual and these lengths were averaged for males and females separately to obtain mean back-calculated lengths at age. These generally agreed with lengths at age predicted by the growth models and show that females grow faster than males after an estimated age of 3 years (Table 3).

Discussion

Swordfish anal-fin spines have been used previously for ageing Atlantic swordfish (Berkeley and Houde, 1983). Ehrhardt (1992) attempted to validate the method by means of marginal increment analysis and reported that growth bands 1 to 4 were deposited annually during the winter months. Results of marginal increment analysis of the present study demonstrated that growth bands for fish 2 to 5 years of age are deposited annually. In both the previous cases, marginal increment analysis was successful in showing the seasonality of band deposition; however, although these results partially validate the method, it cannot be considered successful until all reported ages of each population are validated (Beamish and McFarlane, 1983). Marginal increment analysis has also been successful in elucidating the time of annulus formation in dorsal spines of *Tandanus tandanus* (Davis, 1977). It is unlikely, however, that application of marginal increment analysis to older ages, in which spine growth is considerably reduced, would show any seasonality in band deposition. In general, validation of ages of older fish requires either a mark-recapture study or the iden-

Table 3

Back-calculated and predicted lower jaw fork lengths (LJFL-cm) at age for swordfish, *Xiphias gladius*, from the eastern Mediterranean.

	Back-calculated (proportional formula)		Back-calculated (nonlinear method)		Predicted (standard von Bertalanffy)		Predicted (generalised von Bertalanffy)	
Age	Male	Female	Male	Female	Male	Female	Male	Female
1	—	—	—	—	83.71	82.76	83.79	82.52
2	106.85	108.84	110.82	112.98	109.28	109.99	110.30	112.03
3	126.14	128.44	131.03	136.06	129.36	132.06	129.03	133.00
4	141.34	145.48	146.28	153.79	145.15	149.96	143.81	149.48
5	153.80	159.88	158.22	167.15	157.55	164.46	156.10	163.04
6	165.06	172.64	168.19	178.00	167.30	176.21	166.65	174.52
7	173.32	182.24	177.11	186.76	174.96	185.74	175.87	184.41
8		190.17		193.10	180.98	193.47	184.05	193.04
9		195.16		196.67	185.72	199.73	191.38	200.63

tification of known-age fish in the population (Beamish and McFarlane, 1983).

The present work showed that annuli are formed from late spring to early summer which is the spawning period for swordfish in the Mediterranean (Palco et al., 1981). Since it has been suggested that swordfish use particular spawning grounds in the Mediterranean (Rey, 1988; Cavallaro et. al., 1991), annulus formation may be related to migration of fish to these grounds. A relation between annulus formation and migration has been suggested for the Atlantic swordfish as well (Berkeley and Houde, 1983).

Our findings indicate that anal-fin spines are useful for ageing swordfish. These are important because

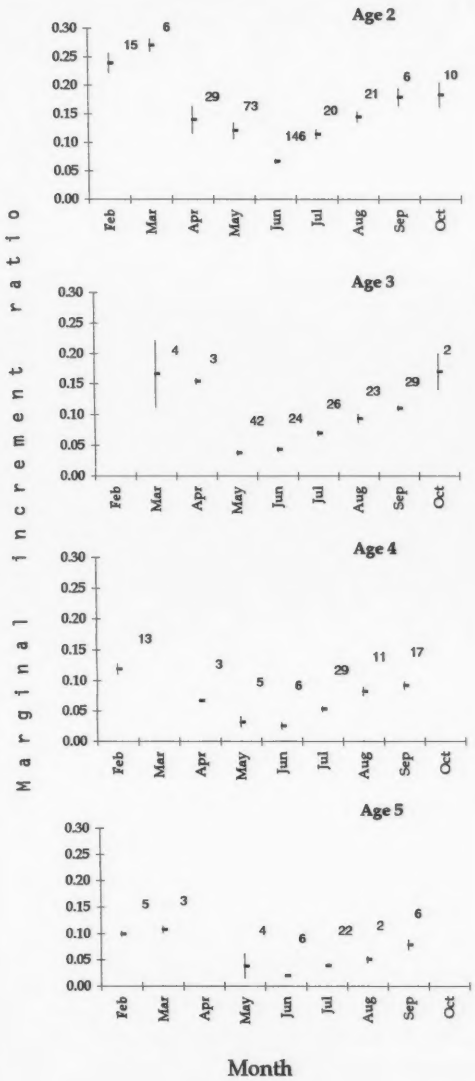

Figure 3

Mean monthly marginal increment ratio for swordfish, *Xiphias gladius*, ages 2–5 from the eastern Mediterranean. Vertical bars represent ±1 SE. Numbers are sample sizes.

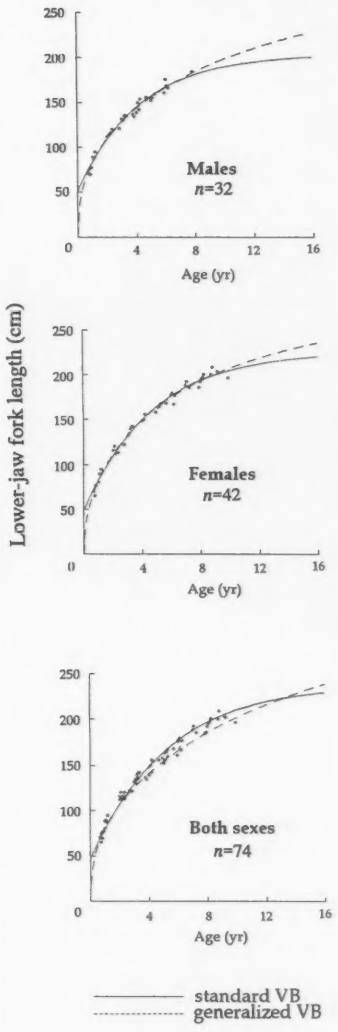

Figure 4

Standard and generalized von Bertalanffy (VB) growth curves for swordfish, *Xiphias gladius*, from the eastern Mediterranean; *n* = sample size.

Table 4

Estimated lower-jaw fork lengths (LJFL to nearest cm) at age for swordfish, *Xiphias gladius*, from studies in the Atlantic (A) and the Mediterranean (M).

	Berkeley and Houde (1983) (A)		Radtke and Hurley (1983) (A)		Wilson and Dean (1983) (A)		Ehrhardt (1992) (A)		Tsimenides and Tserpes (1989) (M)	
Age	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1	97.2	98.0	84	73	116.9	122.9	89.7	89.8	103.2	103.1
2	118.5	119.9	98	85	123.3	130.6	117.0	118.9	129.5	129.1
3	136.0	139.7	110	114	130.2	138.8	137.3	142.9	148.1	149.3
4	150.4	157.8	122	131	137.4	147.5	153.4	161.3	161.4	165.0
5	162.3	174.3	133	147	145.0	156.8	168.9	177.2	170.8	177.3
6	172.0	189.3	143	160	153.0	166.6	181.8	189.6	177.5	186.8
7	180.0	202.9	153	172	161.5	177.1	195.3	204.4	185.2	194.2
8	186.6	215.3	161	183	170.4	188.2	206.1	214.7		

swordfish have no scales and otoliths are not amenable to traditional ageing techniques owing to their small size (Ovchinnikov, 1970; Becket, 1974). Successful otolith readings have been performed only through the application of scanning electron microscopy (Radtke and Hurley, 1983; Wilson and Dean, 1983). Moreover, the use of spines has the advantage that the material can be obtained relatively easily without reducing the economic value of the fish. The main problems associated with the spine method are the existence of multiple bands and the missing first annulus. An experienced reader can overcome the problem of multiple bands by determining whether they continue around the entire circumference of the spine and by recording their distance from the preceding and following annuli. The problem of the missing first annulus in larger fish can be resolved by identifying its position on sections from younger specimens where the annulus is visible. Difficulties in defining the location of the first annulus in older animals have also been reported for Atlantic swordfish (Berkeley and Houde, 1983) and Pacific blue marlin, *Makaira nigricans* (Hill et al., 1989).

Ehrhardt (1992) suggested that the standard von Bertalanffy growth function does not adequately represent the growth of swordfish and proposed the use of the generalized growth function of Chapman (1961). The present estimates of r^2 indicate that both models describe swordfish growth equally well over the age ranges considered and give almost identical results for the first eight years of growth (Fig. 4). Although the extrapolation of regression curves beyond the data is not advisable, it is interesting to note that the generalized model gives much more realistic results for ages less than one because it forces the growth curve to pass close to the origin of both axes. On the other hand, estimates of asymptotic length from this model are questionable because it is unlikely that females have lower asymptotic lengths than males, given that all the large animals in the sample were female. Therefore, the generalized model appears to overestimate asymptotic length (especially that of males).

Although results of both back-calculation methods generally agreed with the values predicted by the growth equations, the estimates of the nonlinear method are in slightly closer agreement (Table 3). The use of a nonlinear function for the LJFL spine-radius relation is preferable because it is more realistic for small animals, which have near zero spine-radius values and very small LJFL values. Ehrhardt (1992) also suggested the use of a nonlinear function to describe the LJFL spine-radius relation.

Growth studies carried out in the Atlantic together with previous work (Tsimenides and Tserpes, 1989) have shown that females grow faster than males (Table 4). Therefore, the calculation of a common growth equation is not valid and may be useful for management purposes only under certain circumstances. However, it should be noted that in previous work (Tsimenides and Tserpes, 1989), lengths at age were overestimated because the position of the first annulus was misidentified.

In the case of swordfish it seems that the use of a relatively wide range of size data and mean values for fitting the growth curves has resulted in relatively unbiased estimates of swordfish growth parameters in the eastern Mediterranean. Since all Mediterranean swordfish are proposed to belong to the same stock (Magoulas et al., 1993), our findings

are appropriate for assessment studies of this stock. The use of the standard von Bertalanffy growth model is recommended for such studies because the generalized model overestimates the asymptotic length, an essential parameter for population dynamics models.

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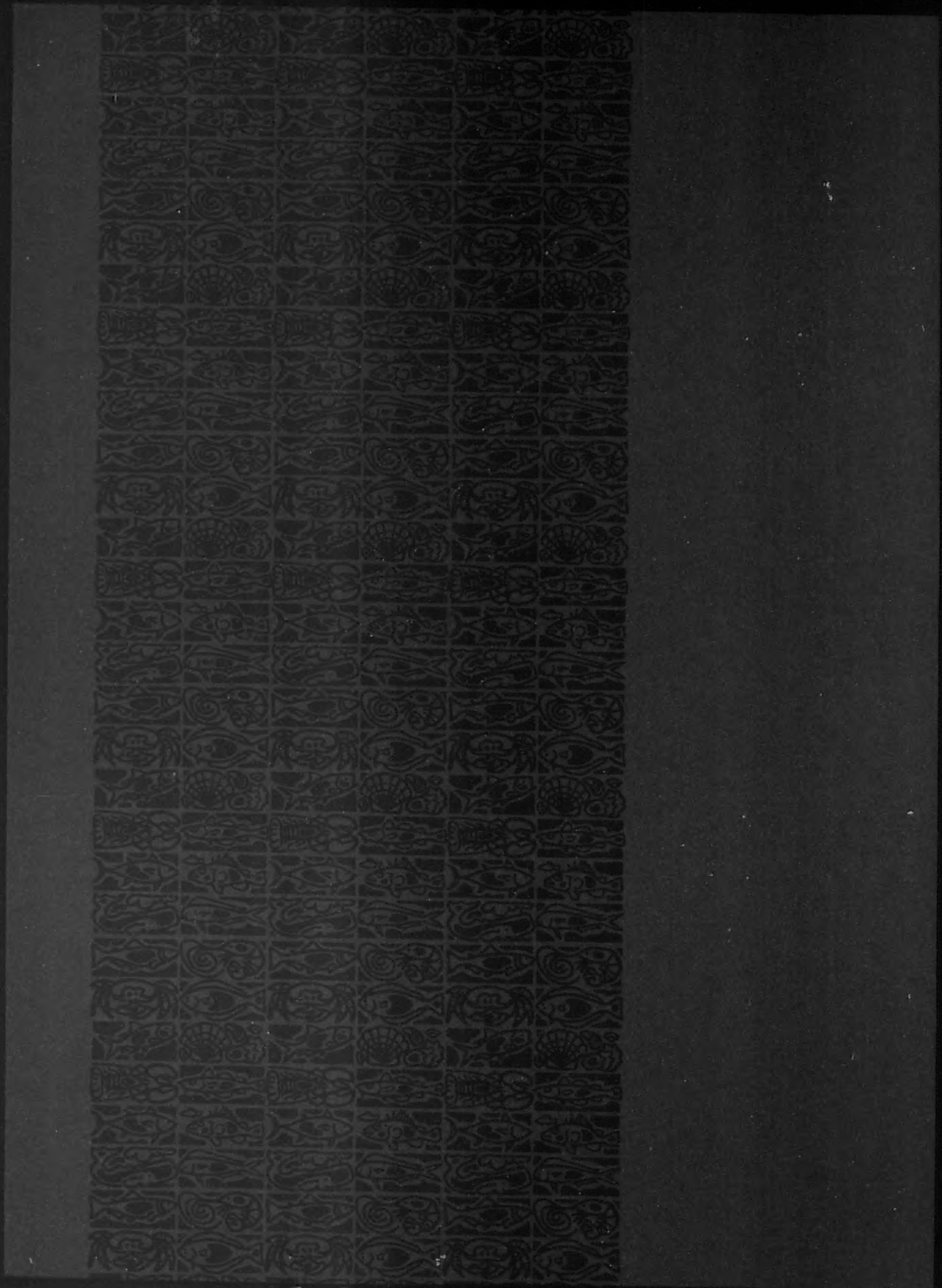
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